The role of demography in the evolution of breeding strategies.

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Originality statement

I, Anna MF Harts, hereby state that the work presented in this thesis is original. I am the senior author and principal contributor of all the chapters. The first four chapters are co-authored by my main supervisor, Hanna Kokko. Chapter 2 and 3 are additionally co-authored with Lisa E Schwanz and Kim Jaatinen, respectively. Chapter 4 is co-authored with Nadiah P Kristensen; for this paper Nadiah also developed and analysed the results of the semi-analytical model. Chapter 5 is co-authored with Isobel Booksmythe and my secondary supervisor Michael D. Jennions; Isobel assisted with compiling data and analysis.

Chapters 1 and 2 have been published in peer-reviewed journals, chapter 3 is currently in press in a peer reviewed journal and chapters 4 and 5 are currently being reviewed by peer-review journals. The chapters are identical to the submitted or published versions.

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Abstract

The five chapters of this thesis all focus on the role of demography in the evolution of breeding strategies.

In the first chapter we explore the role of the adult sex ratio (ASR) in the evolution of mate-guarding duration. Our two models predict male guarding duration to increase with decreasing female availability and increasing number of male competitors. However, with a male biased ASR there are several factors, such as guarding inefficiency and incomplete last male sperm precedence, that prevent the mating system from switching to male monogamy.

The second chapter adresses a situation where females have a larger effect on population dynamics than males (i.e. female demographic dominance). This occurs when female fecundity is relatively independent of male abundance, while male reproduction is proportional to female abundance. Our two simulation models combine dispersal evolution with local adaption subjected to intralocus conflict and environmentally driven sex ratio biases, respectively. Our proof of principle demonstrates that trait evolution is dominated by environments with a higher abundance of females, although this does not imply that all measures of population performance are improved.

In the third chapter we focus on the role of owning a breeding territory for different rates of natal and breeding dispersal. For this we investigate the interplay of the asset-protection principle and the multiplier effect. Our simulation model is set in habitats of spatially varying quality and individuals express dispersal rates based on their life history stage, sex and quality of their habitat. Breeders can evolve high dispersal rates but only if better opportunities are readily available. Non-breeders evolve dispersal mostly in response to competition.

For the fourth chapter we stay with the importance of breeding territories, however we shift our focus to its role as a selective force for early arrival in migratory species. We investigate the role of predation upon arrival at breeding grounds as a selective force for later arrival. We use two models, a semi-analytic and a simulation model, to show that predation upon arrival can select for later arrival however in most cases it also selects for highly synchronous arrival. This high synchrony results in predator satiation and provides safety in numbers.

In chapter 5 we use meta-analyses to investigate three questions related to paternity protection in birds. In socially monogamous birds males are presumed to protect their

paternity with mate-guarding or frequent copulation. We first test if these presumed paternity protection behaviors protect a male's paternity. Our second question focusses on the role of male quality, if females prefer high quality males to sire their offspring then does this mean that high quality males can protect their paternity less? The third question is based on the expected relationship between paternal care and paternity protection behaviors (as a proxy for certainty of paternity), i.e. males are expected to provide more care for offspring they 'think' they have sired. We combine the results of these meta-analyses with the extensive literature on topics frequently associated with paternity in an attempt to provide a general overview.

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Introduction

This thesis consists of five chapters, combined they form diverse examples that together demonstrate the important role of demography and breeding strategies for evolutionary trajectories.

Breeding strategies have evolved to optimise reproductive success dependent on environmental or individual specifics. In the first chapter we focus on a flexible strategy, a male's mate-guarding duration in response to the adult sex ratio (ASR). With a highly biased male ASR one can predict that mate-guarding is a strategy that is likely to result in improved reproductive success, while with a female biased ASR a male is more likely to maximise his reproductive success by foregoing guarding and thus mating with as many females as possible (Parker 1974). This has been the focus of much empirical and theoretical research (e.g. Grafen and Ridley 1983; Yamamura 1986, 1987; Mathews 2002; Kureck et al. 2011), but most research has focused on either pre- or postcopulatory guarding only. In the first chapter we investigate pre- and post-copulatory mate-guarding as a continuum and combine this with the ASR, sperm competition patterns and different windows for fertilization as determinants for mate-guarding duration. We investigate which conditions select for male monogamy and when polygamy results in higher reproductive success.

Reproductive success is one of the most important determinants of fitness together with survival (mortality). If an individual survives to breed and breeds successfully it has gained fitness. As mentioned above the environment is an important determinant of reproductive success, as such many species have evolved local adaptation to a particular environment that allows them to successfully reproduce there (Kawecki and Ebert 2004). This means that dispersal may affect reproductive success if individuals that have dispersed are not adapted to the new environment. The effects of dispersal on local adaptation have been studied intensively theoretically (Ronce 2007), however quite often the assumption is made that males and females are identical in their environmental requirements (Caswell and Weeks 1986; Ronce 2007). In chapter 2 we explore what happens when males and females have different environmental optima or when environments differ in the offspring sex ratio that is produced. The results of this model highlight that these differences can have large consequences under circumstances where females are considered demographically dominant.

Many species require a territory for breeding, and if territories are limited then acquiring a territory is key to reproductive success. Thus a territory could be considered an asset worth protecting. In many species breeding dispersal is much less common than dispersal before breeding (Paradis et al. 1998). Is this sufficient to explain why dispersal is often age-dependent? Dispersal models often consider asexual populations without age structure, while most of the exceptions to this only allow dispersal to evolve for one age class, e.g. only young or older individuals (Johnsen and Gaines 1990; Johst and Brandl 1999). For chapter 3 we designed a simulation model to test whether individuals in possession of a territory are less likely to disperse because they are protecting an asset. Young individuals would then disperse simply because of not having an asset, but another factor, the multiplier effect, could work against this: we expect that offspring born in a good location should be less inclined to disperse. We thus also investigate to what degree territory quality affects the decision for individuals to disperse, i.e. individuals in low quality territories may be more inclined to disperse.

In chapter 4 we stay on the topic of how owning a territory may be beneficial for reproductive success. In migratory birds acquisition of a good territory strongly selects for early arrival (Kokko 1999), while too early arrival also incurs costs (Newton 2008; McKinnon et al. 2010). We look at a factor that has the potential to select for later arrival times but is rarely considered in migration literature, namely predation upon arrival at the breeding ground. Our semi-analytic and simulation model use high reproductive success to select for early arrival while selection for later arrival is via predation upon arrival at the breeding ground but before breeding.

In the final chapter we get back to the role of breeding strategies for reproductive success. Our approach differs from the other chapters in that we use meta-analytic techniques to research the role of paternity protection in birds. In socially monogamous bird species extra-pair paternity is common (Griffith et al. 2002). So, are those costly behaviors that are presumed to protect paternity actually effective? This is the first of three questions we attempt to answer. To explain why females pursue extra-pair copulations the “good genes” hypothesis is often invoked. Based on this hypothesis a female is expected to look for a high quality male to sire her offspring, irrespective if the male is extra- or within-pair (Jennions and Petrie 2000). Our second question investigates if this then implies that high quality males can protect their paternity less because their mates won’t pursue extra-pair copulations. The third question takes paternity protection behavior as a proxy for certainty of paternity, and asks if males that have certainty of paternity provide more care for offspring. Males that are uncertain of their paternity are expected to reduce the amount of paternal care they provide, as caring for offspring is costly (Møller and Birkhead 1993). In the discussion we combine the results of our three meta-analyses with the extensive literature on topics frequently associated with paternity, to provide a general overview.

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Chapter 1 – Understanding promiscuity: when is seeking additional mates better than guarding an already found one?

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Abstract

Paternity protection and the acquisition of multiple mates select for different traits. The consensus from theoretical work is that mate-guarding intensifies with an increasing male bias in the adult sex ratio (ASR). A male bias can thus lead to male monogamy if guarding takes up the entire male time budget. Given that either female or male biased ASRs are possible, why is promiscuity clearly much more common than male monogamy? We address this question with two models, differing in whether males can assess temporal cues of female fertility. Our results confirm the importance of the ASR: guarding durations increase with decreasing female availability and increasing number of male competitors. However, several factors prevent the mating system from switching to male monogamy as soon as the ASR becomes male-biased. Inefficient guarding, incomplete last male sperm precedence, any mechanism that allows sperm to fertilize eggs after the male's departure, and (in some cases) the unfeasibility of precopulatory guarding all help explain cases where promiscuity exists on its own or alongside temporally limited mate-guarding. Shortening the window of fertilization shifts guarding time budgets from the postcopulatory to the precopulatory stage.

Introduction

A simplified view of mating systems and sex differences in reproductive strategies often emphasizes sex differences in the optimal rate of mating, typically higher for males than for females (Gavrilets 2000; Arnqvist and Rowe 2005; Maklakov et al. 2005; Gavrilets and Hayashi 2006). Such a difference cannot, however, explain those monogamous situations that are based on male strategies of paternity protection, which can take the form of extensive mate-guarding (Beecher and Beecher 1979; Birkhead 1979) or mating plugs (Baer et al. 2001; Foellmer 2008; Fromhage 2012). In these cases, it appears to be in the best interest of a male to achieve high paternity with one or few females, rather than attempt maximally many matings.

Clearly, paternity protection and the acquisition of multiple mates can select for different traits. In extreme cases of terminal investment, paternity protection can mean that a male foregoes all chances of finding another female (Fromhage et al. 2005). Mate-guarding, which we focus on here (defined as the close association between a male and female prior to and/or after copulation for paternity assurance), does not always have to be that extreme. Still, there is often a direct trade-off involving time: guarding one female often effectively prevents a male from searching for more of them (Dickinson 1995; Birkhead and Møller 1992; Simmons and Siva-Jothy 1998; Fryer et al. 1999). It follows that if mate-guarding becomes sufficiently extended over time, the mating system becomes socially monogamous (Mathews 2002; note that a socially monogamous system can be genetically monogamous too, if guarding is efficient enough).

Past research has outlined a few principles of whether males should search (leading to a promiscuous mating system) or guard, with a generally emerging consensus that the adult sex ratio (ASR, defined here as males per female) is an extremely important predictor of the mating system (Grafen and Ridley 1983; Yamamura 1986, 1987; Yamamura and Tsuji 1989; Birkhead and Møller 1992). In early models, this insight was expressed rather implicitly: Parker (1974) modelled both precopulatory and postcopulatory guarding, and showed that it is important to consider the time it takes to find a new female (this will obviously take longer if there are fewer females). In his model the time to find a female was modelled as an external constant, thus frequency-dependent selection was not explicitly included. Parker (1974) finished this early paper by noting that once guarding spreads in a population, the advantage of guarding will change.

Grafen and Ridley (1983) took a much more explicit look at frequency-dependent availability of females in their model of precopulatory guarding: the proportion of available (unguarded) females was a function of the guarding criterion used by males. They found that if there are no takeovers (i.e., a male cannot usurp the position of another male currently guarding a female), the system evolves towards male monogamy if (i) the adult sex ratio (ASR) is male-biased, or (ii) if a female-biased sex ratio combines with a slow rate at which the sexes find each other. More recent work has replicated the finding: male-biased adult sex ratios generally select for male monogamy (Fromhage et al. 2005). Thus, theoretical work to date suggests that the prevalence of male monogamy should, at least approximately, reflect the prevalence of male-biased adult sex ratios in nature (e.g. bird populations are often male-biased, Donald 2007, while in polygynous mammals male death rates are typically higher than female death rates, Promislow 1992).

There is some empirical support for the idea that a strong male bias can create monogamy (e.g., Mathews 2002), including curious cases such as monogamy in Schistosoma worms that cause parasitic infections in humans (Beltran and Boissier 2010). The majority of these parasite populations worldwide appear to have a male-biased sex ratio, particularly in early stages of infection (Morand et al. 1993). Empirically, the broad agreement that male biased adult sex ratios can explain male monogamy is complemented by cases where female-biased ASRs are used to explain male roaming (Berger-Tal and Lubin 2011). However, we suspect that in many cases researchers consider monogamy as an exceptional case warranting an explanation, which implies a hidden assumption that promiscuity, being common, is simply the norm and as such requires little attention. If this is the case, a researcher who studies a population where a male-biased ASR combines with promiscuous mating might not realize that this combination ought to be explained.

Mating systems can simultaneously exhibit aspects of promiscuity as well as some mate-guarding. This happens if males spend some of their time budget guarding an already found female, and some of it searching for new females. A closer examination of current theory reveals a lack of studies that ask whether guarding remains temporally limited or whether it evolves to fill the males' entire time budget (male monogamy). Many of the models contrast guarding with non-guarding, but do not include the option of guarding for varying lengths of time (e.g., Sherman 1989; Yamamura and Tsuji 1989; Sandell and Olof 1992; Fryer et al. 1999; Fromhage et al. 2008). In some cases this is justified because male strategies induce permanent monogamy in the form of terminal effort as is the case e.g., for certain spiders (Foellmer and Fairbarn 2003; Andrade and Kasumovic 2005). However the general case remains understudied.

The question 'why don't males more often go for monogamy?' becomes even more important given that existing models do not give males the option to evolve both pre- and postcopulatory guarding. For example, Grafen and Ridley (1983) assume guarding will end at copulation (and as eggs are then fertilized by the guarder, there is no benefit from guarding postcopulatorily to prevent sperm competition), while Yamamura (1986) assumes guarding begins at copulation and the male has the option of letting his mate go before ovipositioning, in which case his sperm can become entirely displaced by another male (100% last male sperm precedence). If males can improve their reproductive success by guarding before as well as after mating, this could conceivably increase the likelihood that monogamy is observed. It appears important to resolve if this leads to a conflict between predictions (male monogamy ought to be common) and reality (male time budgets are not wholly taken up by guarding, instead males often go for multiple females and 'accept' less than 100% paternity with each).

Here we show, in two different models, that the ratio of males to females is an important predictor of the mating system when guarding durations are allowed to evolve, but also that male-biased situations do not automatically lead to male monogamy, even when males can evolve both pre- and postcopulatory guarding. First, in a no-cue situation (males cannot assess temporal cues of female fertility), promiscuity can replace monogamy if there is incomplete last male sperm precedence. This transition happens more easily in populations that are not very male-biased. Incomplete last male sperm precedence in the absence of temporal cues does not, however, produce temporally limited guarding. Second, temporally limited guarding can evolve when time cues of female fertility exist. A short fertilization window shortens postcopulatory guarding but lengthens precopulatory guarding, which also implies that if precopulatory guarding is not possible in a given species, the entire guarding duration can remain rather short. Third, while reductions in female availability (more male biased sex ratios) increase guarding durations, monogamy is not an inevitable outcome of male-biased cases. Instead, promiscuity can exist alongside temporally limited guarding, when at least one of the following conditions is met: (i) guarding is an inefficient way to protect paternity; (ii) some paternity can be gained without guarding; and (iii) the fertilization window is not very brief.

No-cue model

Consider a population with a total of M males and F females. Females oviposit once in a breeding cycle which we take to be of one time unit length. At the time when this happens, she may be guarded by a male, or unguarded. In a no-cue situation, a male who guards a female has no information about the phase of her breeding cycle.

The number of unpaired males, m, equals the total number of males minus the number of pairs p ($m = M - p$); similarly for unpaired females (denoted f, such that $f = F - p$). Pairs form when an unpaired male meets an unpaired female. The rate of two specific individuals meeting is μ, thus the rate with which pairs are formed in the population as a whole is μmf. Paired males guard for a duration G ($G \geq 0$). Pairs decay at a rate p / G, therefore at equilibrium $p / G = \mu mf$. Take-overs do not occur in the model.

Besides a lack of male knowledge about when fertilization takes place we also assume that females are fertile asynchronously. From the male perspective, there is a trade-off between guarding an encountered female for longer, to increase the probability that the next fertilization opportunity happens while he is guarding, and locating new females.

Sperm competition occurs when the male locates an unguarded female that has previously mated but has not yet oviposited. We make the assumption that only the last two males to mate with a female have a chance of fertilizing her eggs. We also assume potentially incomplete last male sperm precedence: the last male to mate with the female fertilizes a proportion P_2 of her eggs. All other eggs are sired by the second to last male (proportion $1 - P_2$). Thus values $P_2 > 0.5$ indicate last male sperm precedence.

The female can yield paternity for the male in two different ways. He can still be the last male to have mated with her when she oviposits, or he can be the second to last male. If he is no longer either male when she oviposits, there is no fitness payoff. A male's fitness increases with the number of breeding cycles completed per time unit, scaled by the fitness reached in each cycle (Supplement I).

The aim is to investigate whether a mutant with a different guarding duration (G) can invade a population with a resident strategy (G_{pop}). For this we assume that the number of mutants is small enough so that it does not influence the operational sex ratio (m/f) of the population. The mutant has a higher fitness (W) than males of the resident strategy when $W(G) > W(G_{\text{pop}})$ (see Supplement I for the solution).

No-cue model: results

The mating system evolves either towards no guarding or male monogamy. Males are expected to evolve longer guarding whenever (Supplement I)

$$P_2 > \frac{F}{M}. \tag{1}$$

Inequality (1) predicts that promiscuity (no guarding) prevails with a female-biased ASR and, in some cases, with male biased ASR. The less paternity is gained by the last male to mate with a female, the larger the range of ASR values (including quite high male biases) that can promote promiscuous matings (Figure 1). Conversely, males benefit from guarding when the chance of locating another female is small (male biased ASR) and the chance of losing paternity if leaving is high (last male sperm precedence).

Thus the males stay with one female if last male sperm precedence, P_2, is high. The immediate effect of reduced cost of lost paternity when leaving should select against guarding. However, a male's own departure decisions can only impact the time he spends as a last male, not anything that happens thereafter (thus it has no impact on the time he spends as a second last male). Being the current guarder of a female at the (unpredictable) time point of siring opportunity guarantees being in the last male role. Thus when being the last male is particularly profitable (high P_2), selection favours prolonging the time being spent in this role.

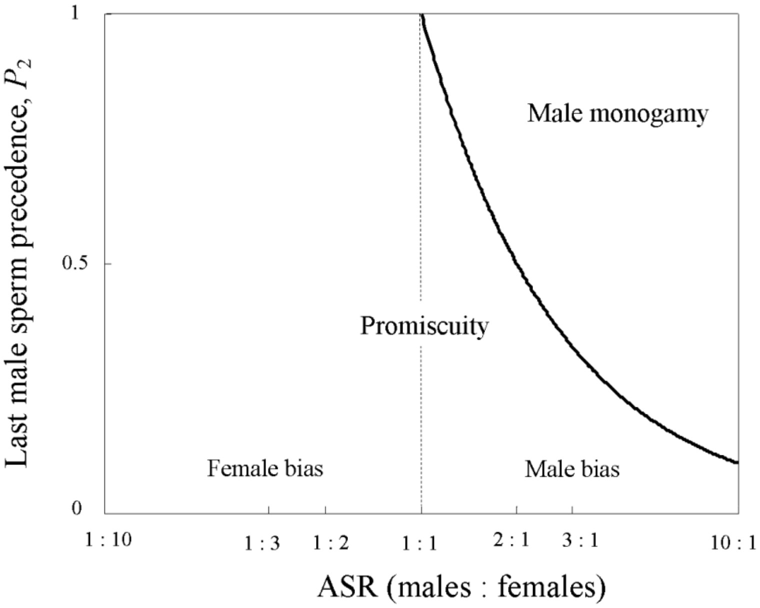

Figure 1. The two outcomes of the no-cue model: male monogamy (guarding fills the entire male time budget) or promiscuity (no guarding). Last-male sperm precedence (P_2) ranges from 0, where the first male fertilizes all the eggs, to 1, where the last male fertilizes all the eggs. The solid line describes $P_2 = F / M$ (inequality 1).

Inequality (1) predicts no region where temporally limited guarding is evolutionary stable: an increasing (or decreasing) population-wide G_{pop} does not select against further prolonging (or reducing) the guarding duration. It is, to some extent, surprising that we find only 'no guarding' (promiscuity) or 'full guarding' (male monogamy) solutions. This becomes understandable, however, once we note that we assumed that a male has no information regarding when a siring opportunity arises. Therefore, if it pays to guard a female at time t_1, there is no reason why he would not benefit from guarding at any other time point t_2. An analogous time invariance is valid in situations where it does not pay to guard. It therefore appears that information about siring opportunities that are female- and time-specific are essential for understanding why males can first guard and then leave a female.

Our second model is motivated by such insights. We seek to examine if some degree of mate-guarding, followed by the departure of the male, can be evolutionarily stable, when information about female timing is available to males. As there is now a specific point in time when an egg is made available, the paternity gain after a male leaves the female will have to be modelled explicitly: a constant P_2 value would not work well as an approximation when males, by guarding longer, can reduce the risk that the egg is still unfertilized and susceptible to being fertilized by another male by the time he leaves the female.

Time-cue model

There are, as before, F adult females and M adult males. Each female produces a fertilizable egg at time point $t = 0$, although it should be noted that this time point is a relative one: females do not breed in synchrony in our model, thus $t = 0$ is the point of the siring opportunity that a particular focal female offers to males. Female breeding cycles are of length 1 (Figure 2). Thus at times $t = 0$, $t = 1, \ldots$, she produces a siring opportunity which can either refer to a fertilizable egg or a clutch of such eggs. Note that oviposition does not have to occur, instead the egg is simply made available for the sire, either internally or externally depending on the species.

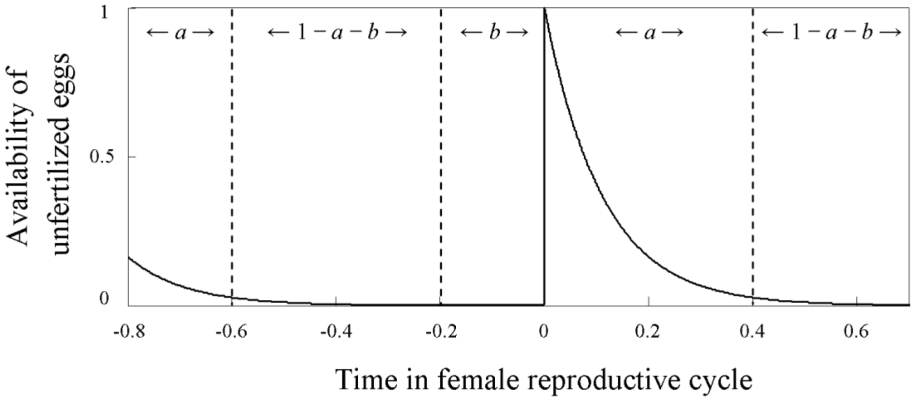

Figure 2. The female reproductive cycle of the time cue model. The female makes a fertilization opportunity available at time points $t = -1$, $t = 0$, $t = 1, \ldots$, and the exponential decline denotes the probability that each egg is still available (unfertilized) at time t. The female is guarded from time $t = -b$ to $t = a$ and remains unguarded for a duration of $1 - a - b$. The value of the exponential function e^{-kt} at $t = a$ indicates the probability that the focal male sired the offspring (assuming $S = 1$, see main text). Here $k = 9$; larger (smaller) values make the curve fall more (less) steeply.

Male strategies are now specified as the duration of time that he spends mate-guarding both before (b) and after (a) the focal point in time where the egg is available (Figure 2). Note that if the total guarding duration $a + b$ reaches the value 1, we have again reached male monogamy.

Consequently, a female breeding cycle is divided into a fraction b which they spend being precopulatorily guarded, a fraction a which they spend postcopulatorily guarded, and the remaining time is spent unguarded (Figure 2). Males have a different time budget (details given in Supplement II) because if $M > F$, not every male can breed every time unit.

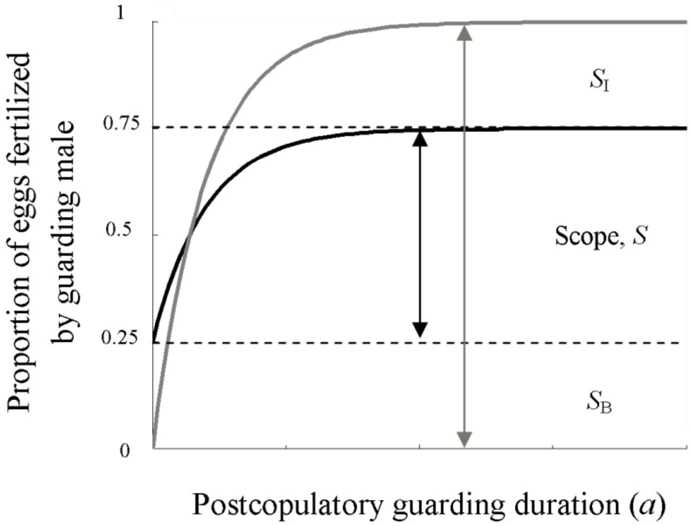

Figure 3. The scope for paternity improvement when it is small, black line ($S = 0.5$ due to $S_I = 0.25$ and $S_B = 0.25$), and large ($S = 1$), grey line. Lengthening the postcopulatory guarding duration increases paternity, but less when the scope for paternity improvement is small.

We assume that if an egg is fertilized while the guarding male is still present, it is fertilized by sperm of this male with probability $1–S_I$, where S_I denotes potential mate-guarding inefficiency. If $S_I > 0$, then even complete monogamy is not sufficient to ensure 100% paternity. On the other hand, we also need to specify the potential for a male to keep fertilizing eggs if he leaves, as his sperm is still present. We denote this potential to fertilize eggs after leaving by S_B, which is the baseline paternity share by this male: if an egg is fertilized, it is sired by the now absent male (who was present at $t = 0$) with probability S_B. Eggs are fertilized at a constant rate k, this means that the probability that an egg is still available to be fertilized at time t if it was made available at time $t = 0$ equals e^{-kt} (Figure 2). The parameter k scales the duration of the fertilization window (see below). The guarding male therefore is the sire with probability $S_B + (1 - S_B - S_I)\ (1 - e^{-ka})$ if his postcopulatory guarding duration is a. This reflects the assumption that paternity equals S_B if males do not guard, and it increases asymptotically towards $1–S_I$ as guarding duration increases. Thus $(1–S_B - S_I)$ is the scope for paternity improvement (S): it indicates the maximum difference in paternity achievable by guarding (Figure 3), so that $S\ (1 - e - ka)$ is the paternity gained by guarding. If guarding is inefficient (high S_I) and/or with baseline paternity (high S_B), there will be little scope for improving paternity by extensive guarding (low S).

Small or large values of k correspond to long and short windows for fertilization, respectively. If $k >> 1$ (and if S is high), a very short postcopulatory guarding duration is sufficient to create high paternity for the male who was present when the egg became fertilizable. We consider very small values (e.g., $k < 1$) unrealistic, as they mean that eggs often fail to be fertilized by the time the female starts a new breeding cycle.

To derive average male fitness in a population where guard durations a and b are in use, we note that a male breeding cycle consists of guarding (duration $a + b$), and a period of non-guarding or roaming (duration T, see Supplement II), during which he can use the siring opportunities that postcopulatorily unguarded females offer. Male fitness is thus the sum of the fitness from guarding and roaming divided by the time it takes a male to complete the breeding cycle. Mutant male fitness can then be compared with average male fitness.

Time-cue model: results

The results (see Supplement II for their derivation) show an overall important effect of the adult sex ratio (Figure 4). Although guarding durations increase with the ASR, the pattern is far more complex than a simplistic expectation of promiscuity at female biased ASR and male monogamy at male biased ASR. Postcopulatory guarding exists for a wide range of ASR values as long as there is sufficient scope for paternity improvement (S), but the duration of this type of guarding often remains limited, particularly if the fertilization window is short (e.g., $k = 100$ in Figure 5 A4). This makes good intuitive sense because it pays to abandon guarding to seek new mating opportunities when most eggs of the current female have already been fertilized, and this happens faster when k is large (short window).

Male monogamy is not a likely outcome of evolution if postcopulatory guarding is the only form of guarding that is possible (Figure 4A). It is not strictly impossible, but it requires choosing parameter values from an extremely favourable and probably unrealistic range. E.g., $k = 5$, which means that it takes the whole unit time to fertilize 99.3% of eggs, obviously leads to longer guarding durations than any of the values in Figure 4A, but it still requires extremely male-biased ratios, $M / F > 29.7$, to yield monogamy if one assumes that conditions otherwise are as favourable to guarding as possible (scope $S = 1$).

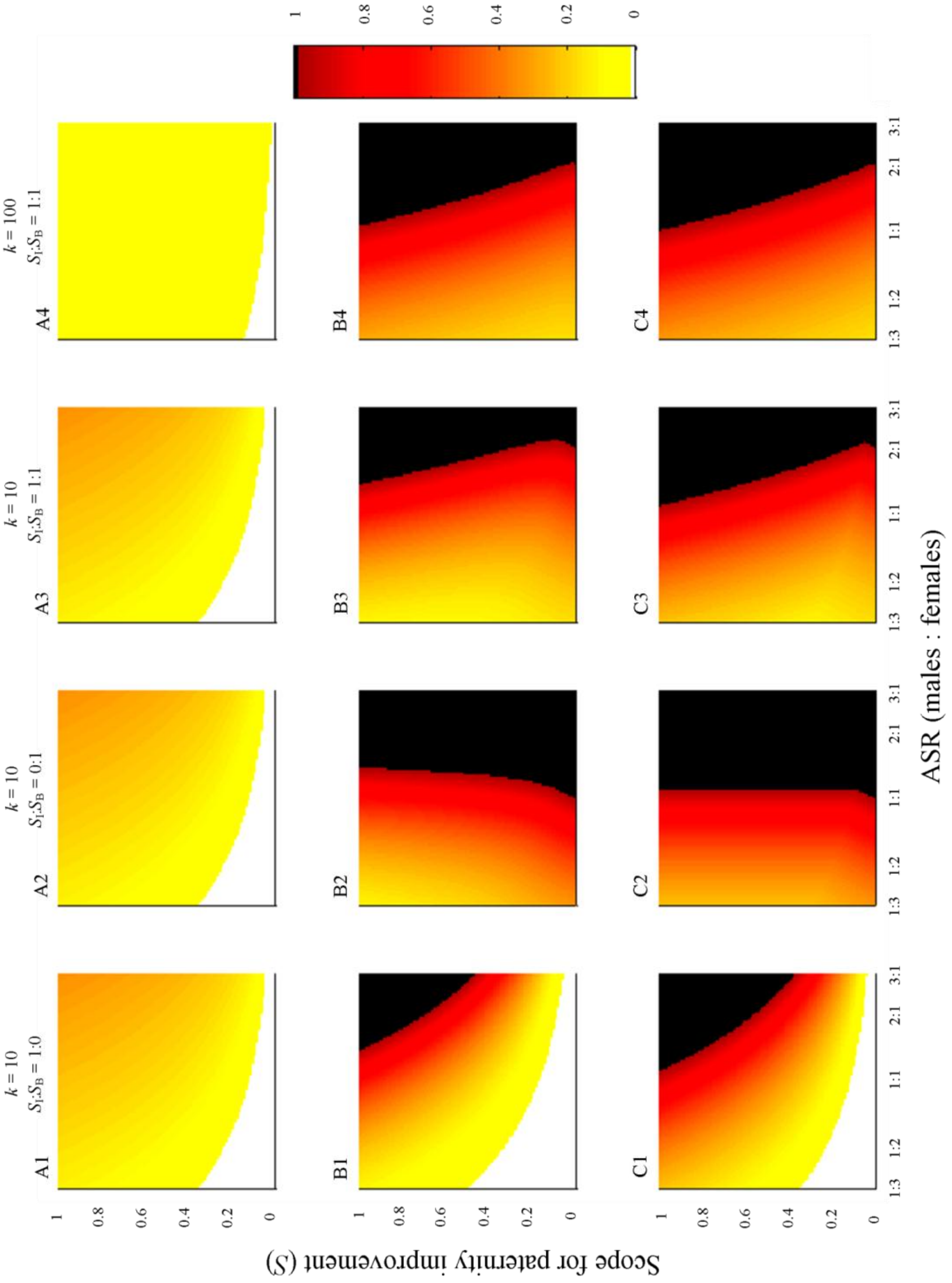

Figure 4. Both pre- and postcopulatory guarding durations increase with the adult sex ratio (ASR) and generally increase with the scope for paternity improvement (S), but the latter rule comes with exceptions in the case of precopulatory guarding. Lighter shades indicate shorter guarding durations (white: no guarding, black: male monogamy). Row (A), postcopulatory duration a*; row (B), precopulatory duration b*; row (C), total duration a*+ b* (capped at 1). Columns differ in the value of *k* as well as whether SI, SB, or both are responsible for a reduced scope (S < 1). For example, the value S = 0.6 results from SI = 0.4 in column 1, from SB = 0.4 in column 2, and SI = SB = 0.2 in columns 3 and 4.

Monogamy evolves far more easily via precopulatory guarding (Figure 4B-C), and the simplistic prediction that any male bias in the ASR is sufficient to trigger it can be recovered for one particular case: when any reduction in the scope for paternity improvement is a result of high achievable paternity in the absence of any postcopulatory guarding (high S_B; Figure 4C2). On the other hand, when there is no such baseline paternity gain ($S_B = 0$) and the scope is instead compromised by inefficient guarding (high S_I, Figure 4C1), guarding durations remain limited even if there is significant male bias in the ASR.

Discussion

Both of our models identify the adult sex ratio as an important determinant of male mate-guarding behavior. More male competitors select for more guarding, and if guarding takes up the entire male budget, the prediction is male monogamy (note that females may still mate multiply as their monogamous mate may die). This central result is in line with earlier work (Parker 1974; Grafen and Ridley 1983; Yamamura 1986, 1987; Yamamura and Tsuji 1989; Fromhage et al. 2005, 2008).

Adult sex ratios are notoriously hard to measure in many systems (Kosztolányi et al. 2011). If male biases in the ASR were rare, the high prevalence of promiscuity would be easily explained, as all models agree that monogamy is unlikely to evolve with female biases in the ASR. However, data do not support a sweeping claim of an extreme rarity of male biases. In principle, any type mortality that targets males or females disproportionately can generate a bias. In the context of predation, Boukal et al. (2008) found male-biased predation to be 2.3 times as common as female-biased predation in a dataset of 81 predator-prey species pairs (ranging from molluscs preying on crustaceans to cases where both predator and prey are mammals).

Although predation data suggests that female-biased ASRs may be more common as a whole than male-biased ASRs (see also Christe et al. 2006), a female bias is clearly not the only possible pattern (Kosztolányi et al. 2011). Factors that impact sex-specific death rates range from immunocompetence (Restif and Amos 2010) to changes in the scheduling of life history events (e.g., growth, Crowley 2000; or migration, Morbey and Ydenberg 2001). Sexes may also differ in their access to prime habitat, which may be primarily used by the larger-bodied or otherwise dominant sex (Marra 2000; Darden and Croft 2008). Given the diversity of factors at play, it is not surprising that the net effect can be either a male or a female bias. In the best studied taxa, i.e., birds and mammals, different patterns predominate: birds typically have male-biased ASRs while mammals show the opposite (Clutton-Brock et al. 1985; Liker and Székely 2005; Donald 2007).

Researchers rarely view a promiscuous mating system as something warranting special attention. While promiscuity can be viewed an adequate null model (Kokko and Mappes 2013), its prevalence should also be contrasted against much theoretical work predicting that any degree of male bias selects for male monogamy. In many cases the 'norm' status of promiscuity might simply reflect its high prevalence among mating systems; it does not mean that one has yet explained why it is so prevalent, given the observed wide variation in adult sex ratios in nature. Thus, the main value of our work is to show that the transition from promiscuity to monogamy is not sharp and does not generally happen at 1:1 adult sex ratio. Instead, we identify several reasons why promiscuity, either in the form of no guarding or temporally limited guarding followed by seeking new females, can persist despite a male bias of the ASR.

If males have no cues of the timing of siring opportunities, all ASR > 1 values select for male monogamy only if there is perfect last male sperm precedence. Because last male sperm precedence is rarely perfect (Birkhead and Hunter 1990), this could be a relatively general explanation for the prevalence of promiscuity in nature. If the last male sires all the young, the profitability of swapping a certain 'last male' status (obtainable by staying with a single female) to the uncertain reward where finding new females combines with some time still spent with the current female as a last male (before she remates when unguarded) depends on the ASR. If there are many new females, the latter is better; if there are few, the certain last male status is the better option. If the last male status is less profitable ($P_2 < 1$), staying with the current female carries a risk that she has mated beforehand, and some eggs are fertilized by a previous male. This decreases the profitability of guarding, and favours promiscuity.

We are unaware of any studies linking last male sperm precedence values to evolved guarding patterns (but see Calbacho-Rosa et al. 2010 for a quantification of paternity assuming that guarding prevents copulations for few or many hours; P_2 was higher when the second male copulated sooner). The obvious empirical challenge is that sperm precedence values are hard to obtain if guarding in male monogamy situations is efficient at preventing any sperm competition from actually occurring. Experimental manipulation of the intensity of sperm competition that would occur should a male abandon a female could prove useful in such contexts.

Our time cue model shows another, diverse set of conditions that allow promiscuity to coexist with mate-guarding. Postcopulatory guarding evolves to correspond, roughly, to the time it takes to 'use up' most of the scope for paternity improvement: if eggs become fertilized quickly, the male can leave quickly, with the exact duration again depending on the availability of new females. Male monogamy does not easily evolve via the postcopulatory route alone. Precopulatory guarding can be much longer, and both types of guarding can exist at either female- or male-biased sex ratios. Their combination can lead to male monogamy, but it usually requires a heavily male-biased ASR, with the exact value depending on the efficiency of guarding, on how much paternity can be achieved without any guarding, and on the length of the fertilization window. There are also situations where precopulatory guarding is impossible or unnecessary, e.g., if mating triggers egg production. In such cases the absence of the precopulatory option again limits the temporal scale of guarding.

Taken together, these results are reassuring: if frequency dependence often leads to temporally limited mate-guarding, we have greater understanding of why real mating systems often combine promiscuity with some degree of mate-guarding. The frequency dependence arises because the relative gains achievable by roaming increase when more males guard (Parker 1974). The same principle explains why some guarding can also exist with female biased ASR.

Of course, there are interactions that our simplistic framework does not include. For example, we have not included differences among males (Birkhead and Møller 1992; Kokko and Morrell 2005). For example, male size has been linked to mate-guarding success (Johnsen et al. 2003; Poirier et al. 2004), to achieving and resisting take-overs (Bel-Venner and Venner 2006) and to a male's ability to monopolize multiple females (Schradin and Lindholm 2011). It is also possible that extensive mate guarding is performed by one male morph only (side-blotched lizards; Zamudio and Sinervo 2000). A polymorphic system can show more complicated dynamics than the convergence of time budgets towards an intermediate value. Still, the essence of the frequency dependence remains the same as in our model, i.e. the identity of the sire, and hence the fitness gains obtained by guarding, depends on how much guarding is happening in the population as a whole.

In a different model of a system without strict polymorphism (humans), Gavrilets (2012) showed that differences among individuals can also favour more guarding in situation where an adult sex ratio of unity would yield zero guarding. His model differs from ours in that it assumes non-linearly increasing gains to a male who reduces his guarding effort.

Hence, guarding is difficult to achieve in his model. Our decision not to include such nonlinearities keeps the interpretation of guarding and roaming more closely linked to the idea of a time budget. In our model each unit of time spent roaming gives the male siring opportunities that simply depend on the availability of unguarded females, not on how much energy (or some other allocatable resource) he has left over from guarding efforts.

Another simplification is that we exclude the possibility that males could guard several females simultaneously; if this is possible, guarding does not produce monogamy. More importantly, existing models, ours included, do not consider that the achievable guarding efficiency might change with the ASR. In many species it has been shown that mate-guarding is not fully efficient and leaves opportunity for cuckoldry resulting in multiple paternity (Alatalo et al. 1987; Birkhead and Møller 1992; Møller and Ninni 1998; Clutton-Brock and Isvaran 2006; Komdeur et al. 2007). We are not, however, aware of empirical studies relating guarding efficiency (or, indeed, extra-pair paternity) to the adult sex ratio. On the other hand, the overall evolutionary outcome (multiple mating by males) does appear to respond to the ASR (e.g., in humans: Kokko and Jennions 2012).

Our model does not comment directly on whether the predicted guarding durations are evolved responses or whether they reflect adaptive plastic male behavior in relation to the ASR (e.g., Parker 1974; Bretman et al. 2011). Within-species variation in the ASR is possible spatially (Carroll and Corneli 1995) and temporally (Forsgren et al. 2004). If individuals can perceive the ASR, or at least a component thereof (e.g., the frequency of being in the proximity of a same-sex competitor), adaptive plastic male behavior is definitely possible (insects: Alcock 1994; Carroll and Corneli 1995; Kureck et al. 2011; crustaceans: Jormalainen 1998; Rondeau and Sainte-Marie 2001; Mathews 2002; mammal: Ramm and Stockley 2009; bird: Møller 1987). For example, males of the snapping shrimp Alpheus angulatus were significantly more likely to abandon recently mated females in experimentally female-biased populations than in unbiased sex ratios, though there was no significant difference in the duration of pairing (Mathews 2002). Excitingly, in the soapberry bug Jadera haematoloma, plasticity in response to experimental manipulations of female density was only expressed by males from a population where the natural social environment is variable (Carroll and Corneli 1995). We expect that similar findings should be possible in vertebrates, where there is documented individual variation in mate-guarding duration (e.g., Komers 1997; Ancona et al. 2010) and variation in reproductive tactics present in a population (Schradin and Lindholm 2011), although in this taxon we are not aware of studies explicitly establishing a link between the ASR and guarding.

Guarding males have been shown to experience costs related to energy expenditure, reduced feeding opportunities, injury, and predation risk (Birkhead and Møller 1992; Komdeur 2001; Cooper and Vitt 2002; Ancona et al. 2010; Rodríguez-Muñoz et al. 2011). Additionally, males and females may have different optimal guarding durations which leads to sexual conflict (Jormalainen 1998; Yamamura and Jormalainen 1996; Westneat and Stewart 2003). None of these details are included in our model: for example, by considering gains per unit time rather than gains accrued during a finite lifespan, we were implicitly assuming that guarding and non-guarding males do not differ in mortality.

Despite these shortcomings, we have been able to identify multiple factors that can explain the combination of some guarding with promiscuity. Frequency-dependent payoffs obtained from guarding can therefore help us better match predictions of the evolution of male monogamy with their real, relatively infrequent, occurrence in nature.

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Supplement I – Solving the no-cue model

First consider the expected number of eggs that the focal male fertilizes in the role of being the last male. During guarding he is always the last male (because take-overs do not occur). The expected time as a last male that his guarding (of duration G) gives him is $G+(\mu m)^{-1}$; this is because after the G units of guarding are over, he is still the last male that the female has mated with until she is found again, which takes $(\mu m)^{-1}$ time units on average. The time it takes for a female to be found by any male is $1/(\mu m)$ while the time it takes for a male to find a female is $1/(\mu f)$. A male's breeding cycle will take $(\mu f)^{-1} + G$ units of time; this is the time it takes him to find one female and to finish guarding her.

After he is no longer the last male to have copulated with the female, he will still be the second to last male who has mated with this female. The expected duration of this state is the length of time the female is guarded by another male, G_{pop}, plus the time she has not yet been found by a third male, $(\mu m)^{-1}$. Note that G_{pop} is not the focal male's own guarding duration but that of any other male in the population; distinguishing between G and G_{pop} is important because a male, by changing his own behaviour, can only influence G but not G_{pop}.

To sum up, a male who guards for G units of time will find a new female every $G + (\mu f)^{-1}$ time units. Each female will give him paternity proportional to $[G + (\mu m)^{-1}]\, P_2 + [G_{\text{pop}} + (\mu m)^{-1}]\,(1-P_2)$. A male's reproductive success (W) is therefore given by

$$W(G) = \frac{\left(G+\frac{1}{\mu m}\right)P_2+\left(G_{pop}+\frac{1}{\mu m}\right)(1-P_2)}{G+\frac{1}{\mu f}} \qquad \text{(S1)}$$

The mutant has a higher reproductive success than males of the resident strategy when $W(G) > W(G_{\text{pop}})$. Solving this inequality results in a simple condition for longer male guarding:

$$P_2 > \frac{F}{M} \qquad \text{(S2)}$$

Conversely, shorter male guarding is favoured whenever $P_2 < F/M$. There is no frequency-dependence leading to temporally limited guarding because P_2, F and M are population-wide constants.

Supplement II – Solving the time-cue model

Female and male time budgets

We assume that the number of males and their mate searching ability means that every female is guarded at the time of the siring opportunity. Below we show why this assumption remains valid at the evolutionary equilibrium even if the ASR is female-biased.

Females spend a fraction b of their time being precopulatorily guarded, a fraction a of their time being postcopulatorily guarded, and the remaining time, $1–a–b$, they spend unguarded (Figure 2). The number of unguarded females (f) is therefore, on average,

$$f = F\,(1–a–b) \qquad \text{(S3)}$$

While females can breed every 1 unit of time, this is not true for males because M does not necessarily equal F. A female who is b time units away from breeding (i.e., has been unguarded for $1–a–b$ units of time) is guaranteed to become guarded by a male. Males, if they are numerous ($M > F$), have to wait on average longer than $1–a–b$ to find a female who is b time units away from giving the siring opportunity. Conversely, if there are relatively few males ($M < F$), their wait time is shorter than $1–a–b$. We denote the time a male spends on roaming by T, thus the length of a breeding cycle for males is, on average, $T+a+b$. The number of non-guarding males (m) in the population is given by

$$m = \frac{T}{T+a+b}M \qquad \text{(S4)}$$

As we did in the non-cue model (Supplement I), we specify p, the number of pairs (guarding male + guarded female) in the population: this obeys $m = M – p$ and $f = F – p$, and can also be expressed as $p = F\,(a+b)$. From (S4) we therefore find the solution for the average male wait time,

$$T = \frac{M}{F} - a - b \qquad \text{(S5)}$$

Note that our model is applicable as long as $T \geq 0$ (i.e., the evolution of a and b cannot proceed beyond the constraint $a+b < M/F$); as we will see, this constraint will be automatically satisfied by evolutionarily stable behaviour.

To derive average male fitness in a population where guard durations a and b are in use, we note that a male breeding cycle consists of guarding (duration $a+b$), during which the male gains fitness

$$x = S_B + S(1 – e^{-ka}), \qquad \text{(S6)}$$

and a period of non-guarding (duration T), during which he can use the siring opportunities that postcopulatorily unguarded females offer. These benefits to 'roaming' males are of magnitude $1 - x = S_I + Se^{-ka}$, and they are offered by f females, distributed over a time of duration $1-a-b$, and competed over by m males. Thus, the fitness accrued during a roaming period of length T is Ty, where

$$y = \frac{f}{m}\frac{S_I+Se^{-ka}}{1-a-b} \tag{S7}$$

is the fitness gain per unit time when roaming, i.e., fertilizing postcopulatory unguarded females' eggs. Using known relationships between F, M, f and m (above), this can also be expressed as

$$y = \frac{S_I+Se^{-ka}}{\frac{M}{F}-a-b} \tag{S8}$$

Male fitness per unit time of his life is

$$W = \frac{x+Ty}{T+a+b} \tag{S9}$$

Using equations (S3)-(S6) and (S8), this expression simplifies to

$$W = \frac{F}{M} \tag{S10}$$

This makes good sense. One male or another gets a total of 1 unit of siring opportunities for each breeding cycle of each female, thus for the average male, the total number of siring opportunities that arise for him, either while guarding or non-guarding, must equal F/M.

Fitness of a mutant male

The above result refers to the population average when all males use a and b as pre- and postcopulatory guarding durations. We now ask what happens when a male deviates from the norm and uses a different value of a and/or b from the rest of the population.

We deal with postcopulatory guarding first, as this is the simpler case. Altering this duration, a, impacts the rate at which a mutant male completes his breeding cycle without altering his wait time (which remains the population average, equation S5). Changing the guarding duration also changes the proportion of eggs fertilized that are made available by the guarded female. Thus, a male with a deviant value of a has his fitness characterized not by eq. (S10) but by (S9) with T and y following the population norm, and a and x having a different value from the resident strategy. Differentiating, we obtain

$$\frac{\partial W}{\partial a} = \frac{\partial}{\partial a}\frac{S_B+S\left(1-e^{-ka}\right)+Ty}{T+a+b} = \frac{F}{M}\left(Ske^{-ka} - \frac{F}{M}\right) \tag{A11}$$

This is positive when $Ske^{-ka} > \frac{F}{M}$, which means that a will increase until

$$a^* = \frac{\ln(Sk\frac{M}{F})}{k} \tag{S12}$$

Note that if $SkM/F < 1$, $\frac{\partial W}{\partial a}$ is negative for all a, thus $a^* = 0$. Thus, a small scope for paternity improvement, a long fertilization window (small k), and a female-biased sex ratio all decrease the likelihood that any postcopulatory guarding will occur.

Fitness calculations for precopulatory guarding are slightly different than those for postcopulatory guarding, because a shorter or longer b cannot be assumed to lead to a different duration of guarding or roaming until a new mate is found, respectively. Instead, given that we assume sufficiently many males that each female will be guarded every breeding cycle, a male who delays guarding (uses a shorter b) will never find a female approaching her $t = 0$. Thus a male with a shorter b than the population average roams continually, gaining fitness through inefficiently guarded eggs as well as those still unfertilized after another male's guarding period is over. A roaming male's fitness accumulates at a rate y per time unit. It follows that if $y > F/M$ (where y follows equation S8), shorter values of b are favoured.

An increased value of b has similarly drastic effects on mate-finding. A male whose b exceeds the population average by an infinitesimally small duration Δb can remove all his waiting time: he accepts females further away from giving a siring opportunity than what is acceptable to other males, thus in the absence of competition, he is guaranteed to find such a female without delay. A male who avoids all waiting by shifting to $b+\Delta b$ (where Δb is approximately zero) has fitness $\frac{S_B+(S)(1-e^{-ka})}{a+b}$ obtained from (S9) with waiting time set to zero. Thus, longer b values are favoured when $\frac{S_B+(S)(1-e^{-ka})}{a+b} > \frac{F}{M}$, and shorter b values are favoured when b leads to $y > F/M$. It follows that selection favours longer guarding b when b is 'too small', shorter values of b when b is 'too long', and these two options collide when

$$\frac{S_B+(S)(1-e^{-ka})}{a+b} = \frac{F}{M} = y = \frac{S_I+(S)e^{-ka}}{\frac{M}{F}-a-b} \tag{S13}$$

Biologically, the interpretation is that when b increases in the population, competitor males spend longer in each breeding cycle, which means that fewer males compete for the eggs that guarding males cannot fertilize (those that have been left unguarded and are still not fertilized, or those that remain unprotected by inefficient guarding). This frequency dependence increases the relative value of going for these eggs (higher y), i.e., roaming. At the point where non-guarding leads to the same fitness as guarding for an infinitesimally longer period than the population average, we have the equilibrium.

$$b^* = \begin{cases} \frac{M}{F}\left(1 - S_I - Se^{-ka}\right) - a & if a^* > 0 \\ \frac{M}{F} S_B & if\ a^* = 0 \end{cases} \qquad \text{(S14)}$$

The sum a^*+b^* (eq. A12 + eq. A14), in cases where guarding occurs, is $\frac{M}{F}(1 - S_I) - \frac{1}{k}$, which gives an intuitive first result: the duration of guarding as a whole increases with the ASR and decreases if guarding is inefficient (high S_I) ; it also increases with the speed of eggs becoming fertilized. We are also finally able to confirm our assumption, that there will always be enough males to begin guarding females who are b^* time units away from offering a siring opportunity, is valid. This follows because the waiting time, $T = \frac{M}{F} - a - b$, reaches the equilibrium value $\frac{MS}{F} + \frac{1}{k}$ if $a^* > 0$, and $T = \frac{M}{F}(1 - S_B)$ if $a^* = 0$. Since both values are positive, the roaming population of males does not 'run out' under either scenario: each male still spends some time $T > 0$ roaming in between two guarding bouts.

There are two special cases. We already noted above that postcopulatory mate-guarding is not selected for when $Sk\frac{M}{F}$. Second, it is also possible that the sum a^*+b^* ≥ 1. This means that males are never selected to stop guarding a single focal female; they persist in guarding from one breeding cycle to the next. This solution implies male monogamy.

Chapter 2 – Demography can favour female-advantageous alleles

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Abstract

When female fecundity is relatively independent of male abundance, while male reproduction is proportional to female abundance, females have a larger effect on population dynamics than males (i.e. female demographic dominance). This population dynamic phenomenon might not appear to influence evolution, because male and female genomes still contribute equally much to the next generation. However, here we examine two evolutionary scenarios to provide a proof of principle that spatial structure can make female demographic dominance matter. Our two simulation models combine dispersal evolution with local adaptation subjected to intralocus sexual conflict and environmentally driven sex ratio biases, respectively. Both models have equilibria where one environment (without being intrinsically poorer) has so few reproductive females that trait evolution becomes disproportionately determined by those environments where females survive better (intralocus sexual conflict model), or where daughters are overproduced (environmental sex determination model). Surprisingly, however, the two facts that selection favours alleles that benefit females, and population growth is improved when female fitness is high, together do not imply that all measures of population performance are improved. The sex-specificity of the source–sink dynamics predicts that populations can evolve to fail to persist in habitats where alleles do poorly when expressed in females.

Introduction

In diploid species, half of the genetic material of each offspring is provided by the male parent, the other half by the female parent. At the same time, the population dynamic properties of populations are more strongly influenced by female than by male performance. This is encapsulated in the concept of female demographic dominance (Crowley 2000), which refers to a set of assumptions where female fecundity is relatively independent of male abundance, while male reproduction is proportional to female abundance. While demographic dominance in this pure form is obviously a simplification (in reality males can have a multitude of effects on female fecundity, Arnqvist and Nilsson 2000; Rankin and Kokko 2007), it holds in an approximate sense widely enough to make the lack of attention to its consequences surprising. Sexual asymmetries in demographic importance are rarely taken into account when studying sexual conflict or primary sex ratios (but see Freedberg and Taylor 2007).

The reason why demographic dominance might be safely ignored is that each offspring inherits equally many autosomal genes from both the male and the female parent. Therefore, even if males and females differ in their life histories or reproductive roles, the overall expectation is equal male and female fitness in diploid species with a 1 : 1 primary sex ratio. As pointed out by Arnqvist (2004), one should therefore express caution when interpreting claims that female evolution elevates their fitness above that of males or vice versa. There is an intuitive sense in which females or males can be argued to 'win' a conflict: consider, for example, intralocus sexual conflict. The evolved allelic values might be closer to the optimum of one sex (also often expressed as a smaller 'lag load', reviewed in Kokko and Jennions 2014). Because of the equal number of genes that pass through males and females to form the next generation, females are typically not assumed to be more likely to 'win' even though they are the main determinant of the size of the next generation.

Here, we build 'proof of principle' models to show that spatial variation in habitat creates scenarios where it is no longer safe to ignore female demographic dominance when arguing about sexual conflict or sex ratio dynamics. Our two models consider subpopulations that are linked via dispersal in spatially varying habitats. This creates conditions where genotype × environment interactions are important for understanding population dynamics. Local adaptation to a particular habitat can lead to a large number of propagules from that habitat; alleles carried by these propagules can come to predominate in the global population (as in source–sink theory, Kawecki 1995). However, this effect can be sexspecific: above-average offspring production requires that females, rather than males, are locally adapted. Therefore, female demographic dominance can, in our two models, result in: (i) more viable females than males (model 1), and (ii) female-biased sex ratios (model 2).

Perhaps surprisingly, we also show that improved female performance does not necessarily maximize global population performance: if females 'win' the conflict in one habitat but 'lose' it in another, then the population as a whole can evolve to be mainly found in habitats where 'females win'. The population will underuse habitats where 'males win', as population growth is predicted to be very poor in areas where only males can thrive. It is notable that this process, where populations evolve to thrive in one habitat only, can occur despite neither habitat being intrinsically more difficult to adapt to than the other; it arises solely owing to sexual conflict.

The models

Our individual-based models of sex-specific local dynamics and dispersal assume sexually reproducing diploid populations where alleles directly impact survival (intralocus sexual conflict model) or offspring sex (environmental sex determination model). Individuals in each model inhabit worlds that consist of two different environments of 50 habitat patches each, creating spatial heterogeneity in a world that totals 100 patches. Each world is initialized by placing 1000 individuals, each an adult female or an adult male (50% probability of being either), onto the patches. As there are 100 patches, each initial subpopulation has a size of approximately five males and five females. All simulations were run for 10 000 generations with 10 repetitions unless stated otherwise. In all simulations, 10 000 generations was found to be sufficient for convergence.

First model: intralocus sexual conflict.

There are three evolving traits in this model. One diploid locus, a, codes for the quantitative trait that impacts an individual's survival in the local patch ('survival allele' for short). This locus is expressed in both sexes as the mean of paternally and maternally inherited allelic values. The two different environments of 50 patches each, which we label environment A and B, differ in the optimal trait value a that leads to highest survival, but this is also sex-dependent (Figure 1; see below). There are also two diploid loci, d_f and d_m, which control the dispersal propensity and are expressed in females only (d_f) or males only (d_m). We assume co-dominance for each of the three diploid loci, such that phenotypes are the mean of the relevant allelic values.

When each simulation commences, individuals are assigned values of a that match the local environmental optima depending on the location of the individual but not on its sex. Individuals are also assigned values of d_f and d_m (these are initially uniformly distributed with mean d_init and a range ($d_\mathrm{init} - \sigma_\mathrm{init}$, $d_\mathrm{init} + \sigma_\mathrm{init}$) around this mean).

Each generation starts with reproduction within each subpopulation (inhabitants of a patch). We specify the number of offspring (N) produced by each subpopulation of F females and M males as follows: if $F \geq 1$ and $M \geq 1$ (at least one individual of each sex is locally present) then $N = 2 + 4Fe^{-cF}$, rounded to the nearest integer; otherwise N = 0. This function, where c is a constant determining the strength of local competition, has the desirable properties of female demographic dominance, in that M does not appear in the equation beyond the $M \geq 1$ requirement, as well as local competition, in that: (i) subpopulations with at least one female always produce at least two offspring (on average one of each sex); (ii) the small subpopulation's output increases if more females are added; but (iii) stronger overcrowding (large F) reduces the subpopulation's output. These rules also imply a kin-selected reason to disperse: a dispersing individual alleviates competition for its relatives (also note that our model ignores some other known reasons to disperse, e.g. inbreeding avoidance, as we assume no cost to consanguineous matings). The model then randomly selects a mother and a father among locally present individuals as parents for each offspring. The offspring inherit their genes according to Mendelian inheritance rules and each offspring has an equal probability of developing as a male or as a female.

Mutations then potentially occur at loci a, d_f and d_m, each allele doing so with probability μ_a or μ_d (the latter value is the same for both dispersal loci). If mutation occurs, the allele's value changes by an amount taken from a uniform distribution with range $[-\sigma_a, \sigma_a]$ (for a) or $[-\sigma_d, \sigma_d]$ (for either dispersal allele). Dispersal alleles that have their new values below 0 or above 1 are set to 0 or 1, respectively.

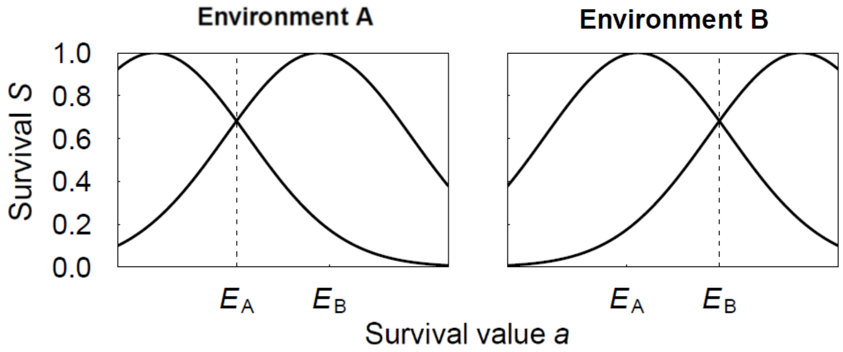

Figure 1. The relationship between the survival allele trait value (a) and survival in each environment. For females E_{opt} is lower than E_i ; for males it is the opposite. All individuals start each simulation with trait values matching either Environment A or Environment B, and there is initially no sex bias in survival. Also note that individuals with $a = E_B$ survive well if dispersed to environment A but only if they are males; similarly, individuals with $a = E_A$ survive well if dispersed to environment B, but only if they are females.

All adults die after reproduction (i.e. we assume nonoverlapping generations). Thereafter, the offspring disperse based on their sex-specifically expressed dispersal probability, which is the mean of their sex-specific dispersal alleles. Dispersing offspring land in a randomly chosen patch among all 100 patches, i.e. dispersers are as likely to experience environment A as B (note that we allow a disperser to land back on its natal patch, to keep this symmetry). Viability selection occurs after dispersal. Survival is modelled according to the conceptual model provided by Cox and Calsbeek (2009): its values are derived as $S = e^{-b(E_{opt}-a)^2}$, where b is a constant, E_{opt} the sex- and environment-specific optimal trait value and a the mean of the individual's survival alleles. Thus, an individual reaches its best survival when its alleles match perfectly the local requirements of the environment, such that $a = E_{\mathrm{opt}}$; mismatches in either direction are associated with reduced survival. E_{opt} is assumed higher for males ($E_{\mathrm{opt}} = E_{\mathrm{i}} + k$) than for females ($E_{\mathrm{opt}} = E_{\mathrm{i}} - k$), where E_{i} refers to the environmental value in environment A or B. Thus, when the model is initiated ($a = E_{\mathrm{i}}$), neither males nor females experience optimal survival, and their survival probabilities are equal (Figure 1). This assumption reflects unresolved intralocus sexual conflict where optimal traits differ between males and females (e.g., Fedorka and Mousseau 2004; Foerster et al. 2007; Prassad et al. 2007; Cox and Calsbeek 2009) as well as between environments. Offspring survival concludes a generation, and the surviving offspring become the breeders of the next generation.

Second model: environmental sex determination

In the second model, we focus on a sex determining mechanism that has the potential to create biased sex ratios: temperature-dependent sex determination (TSD). In this model, the two different environments differ in climate. Environments A and B are now interpretable as 'warm' and 'cold' patches (50 each). Studies of TSD characterize a trait known as the pivotal temperature (T_{piv}), above which offspring develop mainly as one sex, and below which the other sex is overproduced (Bull 1980). Reflecting this, we state that an offspring with T_{piv} will develop as a female according to the sigmoidal probability distribution: $P_f = 1/\left(1 + e^{(T_{piv}-T_{env})}\right)$, and as a male with probability $P_{\mathrm{m}} = 1 - P_{\mathrm{f}}$, where T_{env} is the local temperature (Girondot 1999). Thus, if $T_{\mathrm{piv}} > T_{\mathrm{env}}$ the offspring is likely to develop as a male and conversely, if $T_{\mathrm{piv}} < T_{\mathrm{env}}$, as a female.

The subpopulations are initialized as in the first model, now with pivotal temperature alleles initially set to match the environment ($T_{\mathrm{piv}} = T_{\mathrm{env}}$, within each environment). T_{piv} is the average of the maternally and paternally inherited alleles, which are initially identical. Dispersal probability, as in the first model, is controlled by two diploid loci, one for male and another for female dispersal; an individual only expresses its sex-specific dispersal alleles. Dispersal alleles are initialized and inherited as in model 1. We assume co-dominance for the three diploid loci.

To provide another contrast to the previous model, we now assume overlapping generations. Evolution occurs as follows. Density dependence acts locally on fecundity, such that the number of offspring (N) produced by a local subpopulation is determined by the number of local females (F), $N = Fe^{-cf}$, where c is a constant (and N is rounded to the nearest integer). The function is similar in its gist but differs somewhat from that used in model 1, as there is no requirement of at least two offspring produced by a single female—the current model requires smaller fecundities to sustain a population as generations are overlapping (parents survive). Parents and the genes passed on to offspring are selected as in the first model, but the sex of each offspring is now determined via a genotype × environment interaction (P_f and P_m, see above).

Births are followed by mutation, each of the alleles present in the offspring mutate with a probability μ_d (dispersal) or μ_piv (pivotal temperature alleles). If mutation occurs, the allele's value changes with an amount taken from a uniform distribution within the range $[-\sigma_\mathrm{d}, \sigma_\mathrm{d}]$ and $[-\sigma_\mathrm{piv}, \sigma_\mathrm{piv}]$ for the dispersal and pivotal temperature alleles, respectively (for dispersal alleles, if the new values are below 0 or above 1, they are set to 0 or 1, respectively).

Next, there is mortality in the parental generation: each adult survives with probability $s < 1$ (i.e. we assume overlapping generations) irrespective of sex or any trait values. Thereafter, natal dispersal occurs. Dispersal is global, modelled as in model 1. Thus, a disperser has an equal probability of landing in a 'warm' or a 'cold' patch. After dispersal, all offspring become adults and are thus able to breed in the next generation together with surviving adults.

Note that even though the two models use the same dispersal rules, they differ somewhat in their costs of dispersal. Neither model assumes any other cost of dispersal than an indirect cost due to local adaptation, but in the intralocus sexual conflict model this could have a negative impact on the viability of the disperser, whereas in the current model a locally adapted individual that disperses to a novel environment and reproduces there does not experience a viability cost. Instead, it might pass on pivotal temperature genes that are maladaptive in the current climate, thus the cost is delayed by one generation.

As our aim is to provide two 'proof of principle' examples, we show outcomes based on a single set of parameter values in our figures (with the exception of initial dispersal alleles, as variation in this parameter proves important in model 2). For an additional evaluation of the generality of the results, see supplement III.

Results

First model: intralocus sexual conflict

Regardless of whether simulations are started with low ($d_{\text{init}} = 0.15$, first row, Figure 2) or high ($d_{\text{init}} = 0.85$, second row, Figure 2) dispersal, dispersal alleles evolve to be similar across environments and are somewhat male-biased (Figure 2a,e; note the near identical results between the different dinit runs). Although the proportion of dispersing individuals remains relatively low, this gene flow is sufficient to equalize the survival alleles across environments (triangles Figure 2b,f), thus the population as a whole is not locally adapted (in line with population genetic theory which predicts that relatively little gene flow is sufficient to 'swamp' local adaptation, Mayr 1963; Kirkpatrick and Barton 1997). The evolved survival alleles nearly match the environmental value for environment B.

Given that the allelic values conferring best viability are not only environment-specific but also sex-specific in this model, identical allelic values can produce very different male and female viabilities. The globally evolving trait values predict very high viability for males and low viability for females in environment A, while the same alleles in environment B predict higher female than male viability (Figure 2c,g). This makes subpopulations in environment A unproductive (few females live to produce young), and consequently the total population size evolves to be far greater in environment B (Figure 2d,h).

Environment A males have the highest viability of all individual categories. However, because of the low abundance of individuals in environment A, a randomly sampled individual of the global population has, on average, higher viability if it is a female (mean viability is 0.719 ± 0.005 (s.e.) for all females, and 0.676 ± 0.006 for all males when $d_{\text{init}} = 0.15$; 0.725 ± 0.005 for all females and 0.669 ± 0.006 for all males when $d_{\text{init}} = 0.85$).

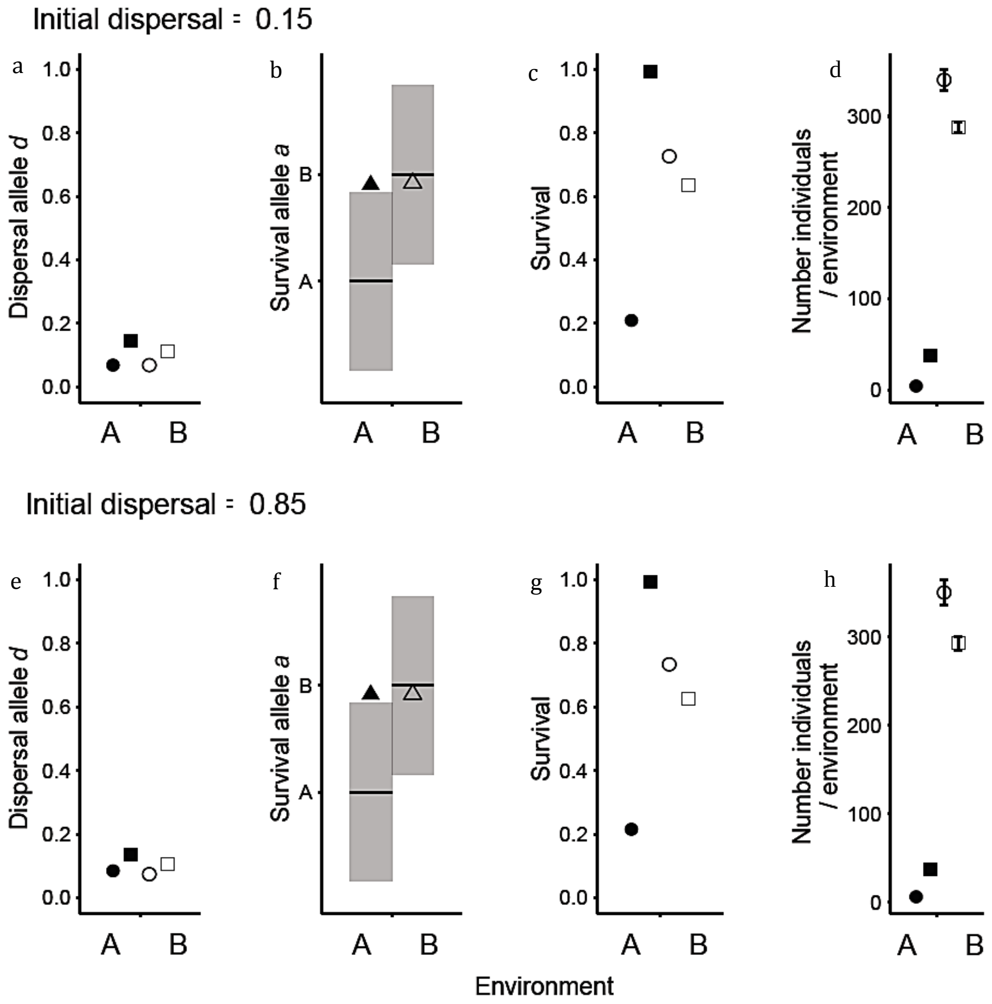

Figure 2. Evolutionary outcomes of the intralocus sexual conflict model, plotted at generation 10000 of 10 independent simulation runs per scenario (except for mean d_{init} = 0.15 where one simulation resulted in extinction in both environments and points are based on 9 independent runs). (a, e) sex- and environment-specific mean of dispersal alleles, (b, f) sex- and environment-specific mean of survival alleles, (c, g) sex- and environment-specific mean of survival as predicted by Figure 1 and (d, h) sex- and environment-specific number of individuals, measured after survival and before breeding. Means ± S.E. given in d and h; in other cases the S.E. are too small to be visible and have thus been left out. Initial dispersal is d_{init} = 0.15 in a–d, and d_{init} = 0.85 in e–f. Black symbols refer to environment A, grey symbols to environment B; squares denote males, circles denote females, and triangles denote both sexes combined. In (b, f) the solid line is the E_{i} value and the dotted lines indicate the sex- and environment-specific optima for a alleles. Also note that E_{A} males have near perfect survival (black squares in (c, g)). Parameter values: $E_{\text{A}} = 5.58$, $E_{\text{B}} = 6.42$, b = 0.7, c = 0.05, $a_{\text{init}} = E_{(\text{A or B})}$, $\mu_{\text{a}} = \mu_{\text{d}} = 0.1$, $\sigma_{\text{init}} = \sigma_{\text{d}} = \sigma_{\text{a}} = 0.05$, and k = 0.74.

Second model: environmental sex determination

Unlike model 1, the environmental sex determination model features two alternative stable states for dispersal. Depending on initial dispersal alleles, the population evolves to low (approx. 10% individuals disperse, $d_{\text{init}} < 0.35$) or high dispersal (approx. 80%, $d_{\text{init}} > 0.4$) (Figure 3a). Both evolved dispersal rates appear sufficient to prevent local adaptation, as T_{piv} evolves to the same value in both environments (Figure 3b). However, the value of T_{piv} differs between runs that lead to low versus high dispersal: when dispersal evolves to be low, T_{piv} evolves to almost match the T_{env} of the warm environment, whereas when dispersal evolves to be high, T_{piv} evolves to the mean of the two environments (Figure 3b).

This leads to a dichotomous pattern in the primary sex ratio produced. If dispersal is low, such that T_{piv} evolves to be near T_{env} of the warm environment, the warm environment produces a slightly female-biased sex ratio and the cold environment greatly overproduces sons. By contrast, high dispersal and the evolved intermediate T_{piv} leads to warm environments overproducing daughters and cold environments equally overproducing sons (Figure 3c). The latter equilibrium leads to a relatively balanced population-wide sex ratio (Figure 3d, high dispersal). The low-dispersal equilibrium, however, shows a similar asymmetry in environment use as was already shown for model 1: there are few females in the cold environment, which renders these subpopulations unproductive, contributing relatively little to the global gene pool.

The situation for the cold environment appears to be a vicious circle: despite being inherently equally suitable as a breeding area, any initial underproduction of daughters in this environment (owing to gene flow from warmer areas) means that few females breed locally. Therefore, the contribution of cold environments to the global gene pool remains weak, and the entire population instead adapts to the warm environment only. The situation remains more egalitarian when dispersal is high, because every population then has many females—either because of overproducing them (warm environments) or because of substantial immigration (cold environments). Under this scenario, every subpopulation continually contributes to the global gene pool.

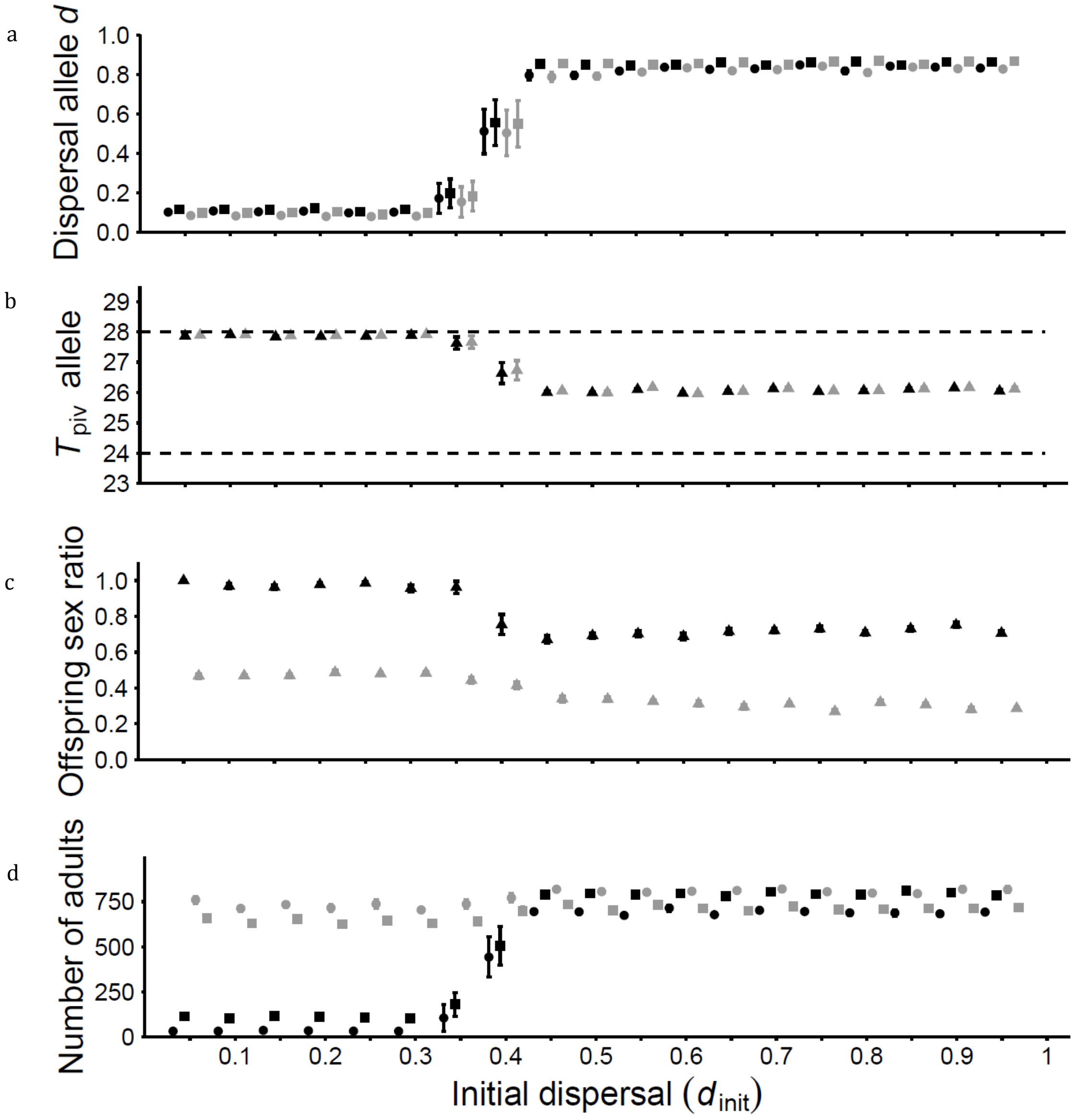

Figure 3. Evolutionary outcomes of the environmental sex determination model. The average (mean ± s.e.) at generation 10000 of 10 independent simulation runs per scenario: (a) dispersal alleles, (b) pivotal temperature, (c) offspring sex ratio (males/total) and (d) number of adults per environment, as a function of the initial dispersal (d_{init}). Cold subpopulations in black and warm subpopulations in grey (T_{env} = 24 and 28, respectively). In (a) and (d) squares denote males and circles denote females. In (b) and (c), triangles denote the mean for each environment. Other parameters: $s = 0.7$, $c = 0.032$, $\sigma_{init} = \sigma_d = 0.05$, $a_{init} = T_{env}$, $\mu_{piv} = \mu_d = 0.1$, $\sigma_{piv} = 0.25$.

Generality

Unsurprisingly, our examples (Figures 2 and 3) require a suitable combination of parameter values. To confirm that they do not represent highly unlikely special cases, we ran 600 simulation trials for the intralocus sexual conflict model and 500 simulation trials for the environmental sex determination model (owing to extinctions, we ran a higher number of simulation trials for model 1). The range of the randomly chosen parameter values for these runs is given in supplement III.

In the intralocus sexual conflict model, these trials showed that female survival evolves to exceed male survival when the two environments vary substantially enough (see supplement III, Figure S1, for details). In the environmental sex determination model, we compared the offspring sex ratio between the cold and the warm environment (supplement III). If the environments did not differ much, high and low initial dispersal led to an identical and simple pattern with T_{piv} equal to the mean for the two environments (supplement III, Figure S2). If environments were sufficiently different, we found two equilibria that depended on initial conditions, similar to our main example of Figure 3. The evolutionary outcome of populations initiated with little dispersal is that the warm environment produced a relatively balanced sex ratio, and the cold populations produced a strongly male-biased sex ratio (squares in supplement III, Figure S2); high dispersal as the initial condition led to a repetition of the simpler pattern where the male bias of cold environments is approximately as strong as the female bias of warm environments (stars in supplement III, Figure S2). Thus, our findings as a whole appear to generalize, as long as there is strong enough environmental variation.

Discussion

Our models include no other asymmetry than the fact that local population growth depends more strongly on the number of females than on the numbers of males (female demographic dominance). Consequently, if a population is adapted, say, to the mean of two environments, it will have some individuals residing in environments that favour females and some in environments that favour males. The former type of environment then becomes more productive as a result of females being the more important determinant of demography. Selection as a whole then becomes disproportionately driven by alleles' success in this environment, and the entire system can begin evolving in a direction where female-advantageous alleles predominate.

It is well known from source–sink theory that evolution of traits can become demographically dominated by populations with above-average productivity (Ronce and Kirkpatrick 2001; Kawecki and Ebert 2004). Substantial gene flow can also lead to one 'generalist' phenotype even when the selective environment differs between populations (e.g., Kisdi 2002; Hendry et al. 2001). We have shown that these principles have significant impacts on trait evolution when there are sex differences in the genotype × environment interaction responses. If the trait impacts survival in a sex-specific manner, or has an effect on the primary sex ratio, then a source–sink structure emerges in environments that do not differ in their suitability *a priori* but simply owing to variance among subpopulations in numbers of reproductively mature females (see also Freedberg and Taylor 2007, for an argument of how this might favour the evolution of TSD *per se*).

Models with coevolution of local adaptation and dispersal very rarely include sexual reproduction (Caswell and Weeks 1986; Ronce 2007), even though local variation in sex ratio have been identified as increasing extinction risks (Aresco 2005; Donald 2007; Lambertucci et al. 2012) and can be a significant source of selection for or against dispersal (Greenwood 1980; Meier et al. 2011). Conversely, models of sexual conflict rarely consider genotype × environment interactions (while mate choice studies do so more commonly, Ingleby et al. 2010). There is clearly more scope for studies linking these fields.

Both of our models show evolutionary endpoints with the following properties: there is a trait that impacts how many females are produced and/or survive to mature, and the trait is subject to a genotype × environment interaction that impacts how many mature females (versus males) will live in each environment. Given that trait evolution is disproportionately influenced by those environments where the genotype × environment interaction favours females rather than males, one might be tempted to conclude that the end result (e.g. in model 1, the average female survives better than the average male) also improves population-wide performance measures such as the ability to persist in a wide variety of environments. However, this is a premature conclusion: if one type of environment becomes disproportionately female-favouring, the importance of adapting to the male-favouring environment can become reduced to such a degree that the population barely persists in these (environment A in our intralocus sexual conflict model, and the cold environment in our environmental sex determination model). This is remarkable, given that we assumed no intrinsic quality differences of these environments: we assumed identical local density dependence across environments, therefore the same number of females led, in principle, to equally good reproduction in either environment.

Our additional result of two alternative stable states, visible in the environmental sex determination model only, is dependent on ancestral dispersal rates that evolve into high or low dispersal. This is in line with previous research, which has identified the potential for alternative stable states based on dispersal rates (Billiard and Lenormand 2005). The mechanism operating in our model, however, differs from earlier studies with coevolution of local adaptation and dispersal (Kisdi 2002; Billiard and Lenormand 2005). While earlier studies document equilibria with much dispersal and little local adaptation or vice versa, we found no evidence of local adaptation in the strict sense (the two environments never evolved clear differences for the alleles used to determine the level of local adaptation, i.e. the survival alleles of model 1 or pivotal temperature of model 2).

Local adaptation is not, per se, prevented from occurring in our models. Separate computer runs with no dispersal (supplement III, Figure S3) lead subpopulations in the two different environments to evolve distinct distributions of T_{piv} or a. This confirms that local adaptation is possible, and that our main results are based on dispersal being sufficient to 'swamp' local adaptation (even the lower dispersal rate of the two alternative equilibria in model 2 was able to do this). Instead, the two equilibria in model 2 reflect differences as to whether dispersal always brings enough females to every type of subpopulation so that no subpopulation ends up too small to contribute to the global gene pool, or whether the local production of females can become compromised and the global process of adaptation is no longer impacted by performance in these environments.

How general are our findings? We assumed a relatively strict form of female demographic dominance, where male availability does not constrain female reproduction unless there are no males locally. Thus, the mating system in our model is likely to be a key factor in the outcome of these models. Had we modelled a strictly monogamous mating system, instead of the polygynous mating system of our models, males and females would have been equally important for population productivity; an emergent pattern where females as a whole evolve higher viabilities is then unlikely (Legendre et al. 1999). For clarity, we also assumed clear differences between exactly two types of environment, local density dependence and global dispersal with no spatial correlation between neighbouring habitats.

Relaxing these assumptions is a clear avenue for further study. Intuitively, it appears that the scale of density dependence will matter. If it were to act on a global scale rather than the local scale as we modelled, then the dynamics would feature even more significant evolutionary effects of female demographic dominance, because highly productive sites can maintain their above-average contribution to the global gene pool. In the opposite case, stronger local density dependence than we included could result in a situation of 'soft selection' (Débarre and Gandon 2011). Under soft selection, improved local adaptation does not translate into higher productivity, as local density regulation equalizes productivity across habitat patches. Consequently, the differing numbers of females that reproduce in each patch have no evolutionary implications. On the other hand, our results are unlikely to depend crucially on our assumption of global dispersal. If individuals do not often disperse to the alternative habitat type, the essence of our model still applies, but with a lower effective dispersal rate. Since the striking effects of female demographic dominance were found irrespective of dispersal rates in model 1, and at low-dispersal rate in model 2, we expect the results to generalize to many spatial structures. The details of such effects, however, would be a fruitful avenue of further study.

It is important to note that dispersal in our models had no direct costs. Any selection against dispersal was based on the possibility that moving leads to maladaptation to the new environment. This is particularly important for understanding the low-dispersal equilibrium in model 2. Dispersal is more likely to lead an individual from award to a cold environment than vice versa, simply because any new offspring is more likely to be born in a warm rather than a cold climate (warm patches have more females than do cold patches). Thus, it is likely to be warm-adapted in its pivotal temperature (see, McNamara and Dall 2011, for a more general version of this argument). In the intralocus sexual conflict model, the mechanism is similar, but impacts the disperser's own viability.

The strong demographic effects of the population sex ratio in a metapopulation could partially explain why primary sex ratios across biota (with any mechanism of sex determination) so frequently depart from 50 : 50 (Bull and Charnov 1988). Even with local adaptation, biased sex ratios are predicted under some selective regimes (e.g. condition-dependent sex ratios, Charnov and Bull 1989; Hulin et al. 2008). However, sex ratios often seem to be even more biased than expected under adaptive explanations, particularly in species with TSD that exhibit extremely female-biased sex ratios in some populations (Bull and Charnov 1988; Hulin et al. 2008). Our results indicate that female-biased sex ratios can be expected across a range of dispersal levels, either owing to a lack of local adaptation or to demographic swamping by adapted populations and restricted gene flow from populations in male-producing climates, even if other suggested mechanisms such as cultural inheritance (Freedberg and Wade 2001)are absent. Note that we have not included selection for more variable sex ratios, which may also impact population persistence if there is a frequent need to colonize empty patches (Freedberg and Taylor 2007).

In conclusion, our results demonstrate a potentially underappreciated role for female demographic dominance in trait evolution under sexual conflict. We have examined this principle under two very different scenarios, but we suspect that the finding can be quite general: whenever local population productivity is more dependent on the production or performance of females than of males, and there is spatial variation with different subpopulations contributing to the global gene pool, we can expect sexual asymmetries to emerge where female-beneficial alleles can be said to have an upper hand. Simultaneously, however, our results warn against any naïve expectation that this necessarily maximizes global population performance: our examples also show that the conflict can cause severe failure to adapt to some habitats despite these being, in principle, adequate for breeding.

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Supplement III – Supplementary simulations

Our supplementary simulations used randomly chosen sets of parameter values with values chosen as indicated in Table S1.

Supplementary simulations			
Intralocus sexual conflict		Environmental sex determination	
Parameter	Value	Parameter	Value
E_{diff}	[0, 2]	T_{diff}	[0, 8]
E_{A}	$6 - E_{\text{diff}}/2$	T_{env} of cold habitat	$26 - T_{\text{diff}}/2$
E_{B}	$6 + E_{\text{diff}}/2$	T_{env} of warm habitat	$26 + T_{\text{diff}}/2$
k	[0.7, 1.0]	s	[0.55, 0.85]
c	[0.025, 0.075]	c	[0.015, 0.049]
σ_{init}	[0.025, 0.075]	σ_{init}	[0.025, 0.075]

Table S1. Parameter values used in supplementary simulations; parameters not mentioned are given in figure legends. A range is indicated as [minimum value, maximum value], and the value for each parameter set sampled rom a uniform distribution spanning this range.

Details for supplementary simulations: Intralocus sexual conflict model

We chose 600 sets of random parameter values (Table S1) and ran two independent simulation runs for each, one initialized with low (d_{init} sampled from a uniform distribution with range [0.1, 0.1 + 2σ_{init}]) or high dispersal (d_{init} sampled from a uniform distribution with range [0.8, 0.8 + 2σ_{init}]). As no clear differences evolved between outcomes of different dinit values apart from a stronger tendency to go extinct with high initial dispersal, the outcomes from surviving populations are pooled in Figure S1. Mean female survival clearly exceeds mean male survival once environments differ substantially enough.

Details for supplementary simulations: Environmental sex determination model

Each of the 500 trials consisted of two independent simulation runs that used otherwise identical parameter values (given in Table S1) but one started with low dispersal (d_{init} sampled from a uniform distribution with range [0.2, 0.2 + 2σ_{init}]), the other with high (d_{init} sampled from a uniform distribution with range [0.8, 0.8 + 2σ_{init}]). The evolved outcome confirms the generality of Figure 3 as long as the environments differ substantially enough (Figure S2).

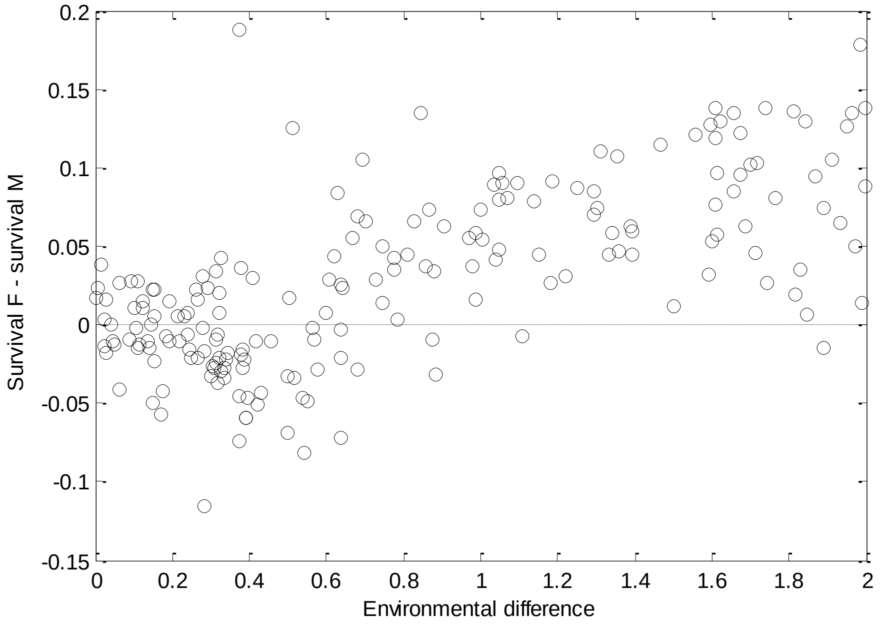

Figure S1. Difference between mean female and mean male survival for the 600 random trials, plotted against the environmental difference between the two habitats (E_{diff}). Only data from surviving populations are shown (at generation 10000).

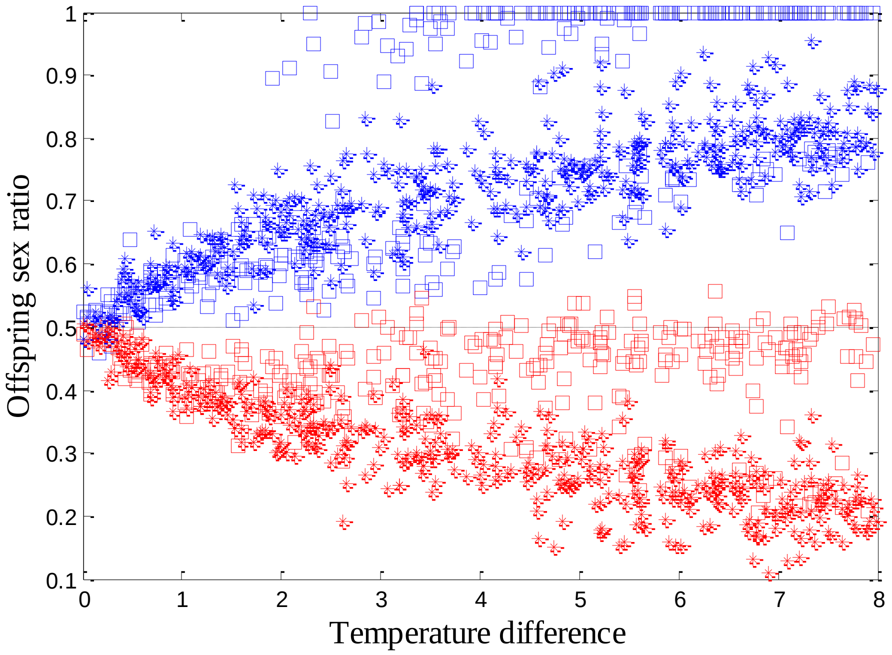

Figure S2. Offspring sex ratio (males/total) at generation 10000 in the cold and the warm environment of the 500 random trials, plotted against the temperature difference between the two habitats, T_{diff}. Stars, high initial dispersal; squares, low initial dispersal. Red symbols are used for the warm environment and blue symbols for the cold environment.

Simulations without dispersal

Locally adapted populations evolved (Figure S3: left, intralocus sexual conflict model; right, environmental sex determination model) in simulations without initial dispersal and where dispersal was not able to evolve ($d_{\text{init}} = 0$ and $\mu_d = 0$).

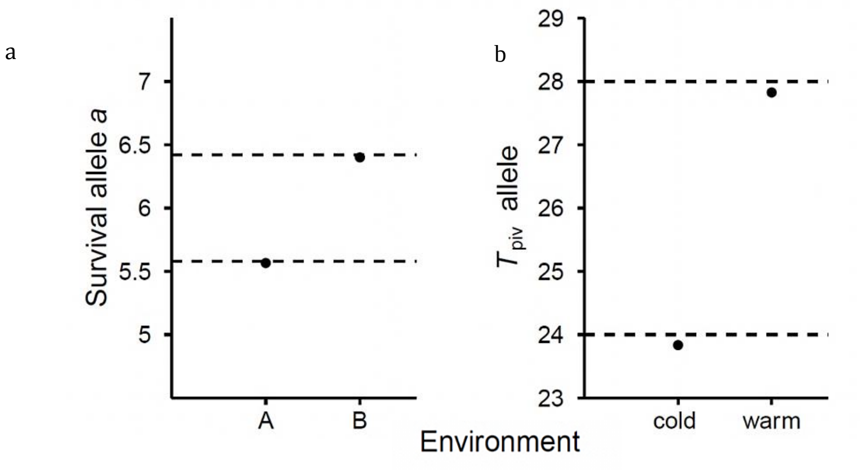

Figure S3. Mean allele values at generation 100 based on 10 independent simulation runs for the survival allele (a) on the left and the pivotal temperature allele T_{piv} on the right. Since without dispersal extinctions occur more often, we recorded allele values at a lower number of generations than in our main findings. The dotted lines represent the respective local environments (environment A and the cold environment are the lower lines, respectively).

Chapter 3 – Evolution of natal and breeding dispersal: when is a territory an asset worth protecting?

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Abstract

Evolutionary models of dispersal frequently lack explicit reference to the age or sex of the individuals that disperse. This contrasts with reality where dispersal behavior strongly depends on individuals' state, including age. To study why natal dispersal occurs more commonly than breeding dispersal, we investigate the interplay of two categories of explanation: the asset-protection principle (APP) and the 'multiplier effect' (ME). The APP states that adults in possession of territories should be more reluctant to disperse. According to the ME the simple fact of being born tells individuals that the site is of high quality, which may promote philopatry. Our model is set in habitats of spatially varying quality and individuals express different dispersal rates depending on state (life history stage, sex and quality of residential habitat). The model considers the accuracy of information about habitat quality, the proportion of good quality habitat and the magnitude of habitat quality variation. We show that the predictions of the APP hold, but only when the 'invisible' asset of likely future prospects in the current habitat is taken into account. Effects of the ME are consistently harder to detect, mainly due to density dependency overriding the benefits of habitat quality. We predict higher natal than breeding dispersal when territorial vacancies are scarce, and more variable breeding than natal dispersal when they are common.

Introduction

Dispersal is known to be driven by a range of selection pressures, such as kin competition, inbreeding avoidance and escaping negative effects of spatiotemporal variation in habitat quality (Hamilton and May 1977; Johnson and Gaines 1990; Bowler and Benton 2005, Roze and Rousset 2005; Ronce 2007; Clobert et al. 2012; Duputié and Massol 2013). General models of dispersal typically consider the effects of these factors in asexual semelparous populations; when considered, the most common categorization of the individuals is their sex (Johnsen and Gaines 1990; Gros et al. 2009; Shaw and Kokko 2014). Much less attention has been paid to whether dispersal strategies of individuals depend on age or other stages they have reached in their life history (Starrfelt and Kokko 2012), e.g., whether the individual already possesses a breeding territory or whether they have bred successfully (Switzer 1993; Johst and Brandl 1999; Arlt and Pärt 2008; Edelaar and Bolnick 2012).

Dispersing prior to ever breeding, i.e. natal dispersal, is in many species more common than breeding dispersal, which occurs between two breeding attempts (Greenwood and Harvey 1982; Paradis et al. 1998; Johst and Brandl 1999). Therefore, assumptions of age- or state-independent dispersal clearly contrast with reality. For example, in an extensive British bird dataset, natal dispersal distances were larger than breeding dispersal distances for 61 out of those 69 species for which sufficient information of both natal and breeding dispersal was available (Paradis et al. 1998). Some stage-structured dispersal models simply take such patterns as given, such that only juveniles are assumed to disperse (e.g. Ronce et al. 1998, 2000; Schjørring 2002). The focus of this study is on elucidating *why* adults are often less prone to leave. To do so we investigate the interplay of two relevant factors: the asset-protection principle (APP; Clark 1994), and the implicit information of site quality obtained by residing at a natal site ('multiplier effect' i.e. ME; McNamara and Dall 2011; foreshadowed by Hastings 1983).

In territorial species, breeding dispersal implies that the individual foregoes an opportunity to breed in a territory that it already 'owned' (Belichon et al. 1996; Danchin and Cam 2002; Doligez and Pärt 2008), while natal individuals do not generally possess a breeding site yet. It is therefore tempting to explain the relative scarcity of breeding dispersal with the asset-protection principle (Clark 1994). This principle was originally phrased in the context of antipredator behaviour, but it generalizes to various situations where an individual can risk losing what it already has. In the current context, adults in possession of a site or territory have more to lose if they disperse than juveniles (see also Morris 1982 for a similar statement). However, the accuracy of information about one's territory, as well as the magnitude of habitat quality variation might both matter, as a poor quality territory may not qualify as an asset worth protecting (if the individual perceives this accurately enough). Because individuals on poor sites are then expected to show breeding dispersal (Krebs 1971; Mestre and Bonte 2012), spatial habitat quality variation could therefore, as a whole, promote dispersal.

The multiplier effect (ME, McNamara and Dall 2011), in turn, refers to the fact that if good habitats lead to better reproduction than poor habitats, then an individual is disproportionately likely to be born in a good habitat (relative to the global availability of such habitat). The interesting corollary is that the simple fact of being born gives an individual implicit knowledge that its local habitat quality is likely to be above the average of the entire landscape — even if no other cues exist (for earlier treatments of this effect, though without use of the term 'multiplier effect', see Hastings 1983; and Holt 1985). If juveniles stay at 'home' and eventually breed there, this knowledge effect could extend to adult life. The multiplier effect can thus as a whole select against dispersal if habitats vary in quality (Hastings 1983; Holt 1985; McNamara and Dall 2011).

We therefore have a rather contrasting set of predictions, that appear to be based on starkly different assumption structures. If individuals can condition their dispersal on spatial variability (McPeek and Holt 1992; Leturque and Rousset 2002; Rodrigues and Johnstone 2014), we expect a different set of responses than the simple dispersal-reducing effect of spatial variability when explicit habitat assessment is impossible (Hastings 1983; Holt 1985; McNamara and Dall 2011). Real life is unlikely to be black and white with respect to information use, however. In reality, assessment of habitat is a continuum ranging from cases where the only source of information is the demographic effect (disproportionate production of individuals in good sites) that a natal site of a randomly chosen young individual tends to be of above average quality, to cases where individuals can immediately assess their current habitat in an error-free manner.

Thus, we suspect that the evolved dispersal rates of individuals differing in state (especially with respect to their assets) will depend on exactly how well they are informed about their current habitat quality. Past models have tended to assume that all individuals either have this information or that they do not; they also often assume only one dispersal event and discrete generations, which effectively prevents comparing the dispersal behaviour of individuals with and without assets. Overlapping generations thus offer intriguing ways to combine the APP with the ME, not least because information provided by the ME can only exist for those individuals who have not yet dispersed. To consider all these processes requires a model where dispersal propensity can depend on life stage, where habitat quality variation ranges from absent to substantial, and where different accuracies of habitat quality assessment, including no perceptual ability, i.e., all 'knowledge' is evolutionarily acquired.

The model

Addressing the impact of asset-protection and multiplier effects requires considering spatially varying habitats, and to be able to explicitly contrast natal and breeding dispersal requires overlapping generations. Habitats in our model can therefore be either good or poor, and this impacts the reproductive success of their inhabitants. Habitats consist of breeding sites (territories) which have three types of residents: a breeder ‘owns’ the territory, but there can also be non-breeders who in turn come in two flavours: ‘natals’ if they have not yet dispersed, and ‘floaters’ if they have left their place of birth. We differentiate between natals and floaters because if the multiplier effect is strong, selection should favor expressing two different dispersal rates depending on whether individuals are still in the habitat that produced them. Breeders are expressing yet another dispersal rate.

We assume that individual breeders with a territory (owners, ‘breeders’) cannot be ousted, thus some breeding success is guaranteed for them, but with spatial variation in habitat quality, being an owner (of a potentially poor territory) also means foregoing chances of competing for other (potentially better) territories. Natals and floaters acquire breeding territories at a rate of territories becoming vacant due to mortality and dispersal of breeders. Competition is concentrated on the site they reside in, but with some additional probability of outcompeting others at sites that aren’t their focal one. To evaluate the role of direct cues of habitat quality, we assume that individuals may have either perfect, imperfect or no knowledge of the quality of their local environment, beyond the evolutionary knowledge offered by the multiplier effect.

Our individual-based simulation model assumes s breeding territories, each being potentially occupied by one breeding male and one breeding female and a number of non-breeders of both sexes. A proportion z of breeding territories is considered to consist of good habitat and the remainder is considered poor habitat. All individuals are assigned to a territory but only breeders can reproduce. Within each sex, an individual’s state is thus characterized by its life history stage (natal, floater, breeder) and type of habitat (good, poor).

A simulation is initiated by creating N diploid breeders, each a male or a female (50% probability of being either). Every individual has six diploid loci that determine its dispersal probability d ($0 \leq d \leq 1$) conditional on its life-history stage (natal, floater, breeder) and its perceived current habitat quality (good or poor; note that this may differ from reality if there is perceptual error, see below). The individual disperses with a probability equal to the mean of the two alleles at the appropriate locus. Alleles were initiated as uniformly distributed random numbers chosen from the range [0, 1].

In the first generation the breeding territories are filled in a quality-dependent manner which also maximizes the number of pairs that form and minimizes the number of cases where a territory is occupied by either a female alone or a male alone: males and females take turns, first choosing good territories until none are available, then choosing poor territories, but always preferring a site with a mate over a site without one. This simple procedure leaves initially approximately $s{-}N/2$ poor territories empty. The number is approximate because the number of males is not necessarily exactly equal to the number of females. For example, if s = 700, z = 0.5 and N = 1000, we have approximately 500 males and 500 females, which will fill all the 350 (sz) good territories and approximate 150 of the poor ones.

Each generation has the same sequence and timing of events. A generation starts with reproduction within each territory that has both a male and a female breeder; it is followed by mortality, and then two steps during which individuals can change their location: a dispersal stage, and a stage of competing for breeding sites. During the latter, an individual can acquire the status of a breeder if previous breeders have died or dispersed.

Reproduction occurs in those territories that have at least one individual of each sex (only the breeding pair can produce any young; see below for more information on breeding pair formation). The number of offspring produced follows a Poisson distribution with mean λ in poor territories and $\alpha\lambda$ ($\alpha \geq 1$) in good territories, thus good territories have higher reproductive success by a factor α. Offspring sex is randomly determined. In addition to Mendelian inheritance at all loci, each of the dispersal alleles mutate in offspring after birth with probability μ. A mutation changes the allele's value with an amount taken from a normal distribution with range $[-\sigma_d, \sigma_d]$. Allelic values that fall below 0 or exceed 1 are set at 0 or 1, respectively.

Mortality is set to occur after reproduction, with all individuals having the same probability (m) of surviving to the next generation. Survivors then assess their habitat. An individual's perception of a habitat may differ from reality, and we model the error as ε (with $0 \leq \varepsilon \leq 0.5$). Here $\varepsilon = 0$ represents perfect perception of habitat quality such that an individual residing in good habitat always perceives it as good, and vice versa. At the other extreme, $\varepsilon = 0.5$ implies that there are no effective cues as an individual is just as often wrong as it is right. Individuals that misperceive the quality of their local territory use the dispersal allele for the habitat type they are not in. For example, if a natal individual residing in a good quality territory makes a perception error in assessing the territory (it does so with probability ε) it will disperse based on the 'natal in poor habitat' dispersal locus.

The dispersal stage makes dispersing individuals land in a randomly selected territory, thus if z = 0.5 there is an equal chance of landing in a good or a poor territory. For simplicity we do not exclude the possibility of landing in the territory the individual dispersed from; the large number of sites makes this in practice unlikely. Breeders (and natals) that disperse become classified as a floater until they (again) find a breeding territory.

Following dispersal, there is competition for breeding sites, which is shorthand for competing to acquire the status of a breeder at a site. Like dispersal, this can lead to shifts in individuals' location, but these are now movements that directly target vacancies that have been created by mortality or breeder dispersal. Some of the breeding territories have become vacant for potential breeders of a given sex. We assume that non-breeders (natals and floaters alike) can perceive vacancies in more than one territory, but their competitiveness for a vacancy is elevated by a factor $r > 1$ (which we call the locality factor) if the vacancy occurs in the territory where they currently reside. For example, if r = 10 and the former female breeder has died, the local female non-breeders, if there are any in the focal territory, are each equally likely to acquire the territory, and their probability of doing so is 10-fold that of any non-breeders that currently reside elsewhere.

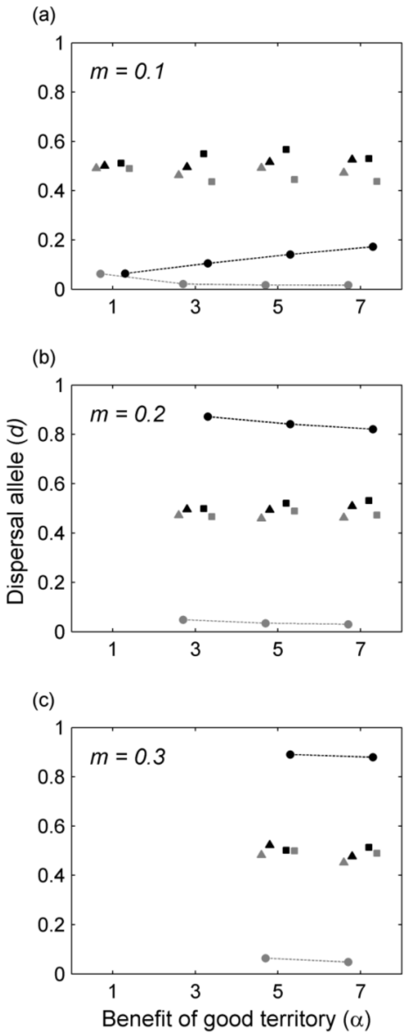
Competition for sites occurs in a specific order, this order is designed to maximize the number of breeding pairs. First, males compete for territories without male breeders that have at least one local female (breeding or non-breeding). Secondly, males compete for the territories that lack a male breeder but have no local females (but at least one local male who is not yet assigned breeder status). Last, males compete for completely empty territories. Nonbreeding females compete after males have taken up breeding territories: first for territories that lack a female breeder but have a breeding male and local non-breeding females. Secondly, females compete for territories without any type of female but with a breeding male. Thirdly, females compete for territories without a breeding male, and thus also lack non-breeding males, but with local non-breeding females. Finally, females compete for territories that have no males or females of any type. Individuals that acquire a breeding position change state to a breeder; the non-breeders retain their current state (natal or floater) and location as they may compete for a breeding site again in the next year if they survive to compete again. A breeding pair will breed again in the next year unless one or both members of the pair disperse or die.

Because natal philopatry may lead to competition between kin, we ran additional simulations in which we 'shuffled' all individuals within their category (natal, floater or breeder), sex and territory quality class (Poethke et al. 2007). In this exercise individuals' current locations are swapped within each class, which keeps the numbers of individuals per site intact but cancels all kin structuring in the population. For example, a female natal individual in a good territory randomly takes the place of another female natal individual in a good territory, meaning that the numbers of individuals in each category, sex and territory quality class are identical before and after shuffling, while the genetic structure of the population has changed. Comparing the results then allows assessment of the effects of kin competition on the evolution of dispersal rates. The results of these additional simulations can be found in supplement IV.

All simulations were run for 5000 generations, which proved sufficient to yield no further change on average. All simulations led to identical results for both males and females, wherefore only one sex is shown in the figures below (where applicable). We used the following parameter values as a 'baseline', i.e. unless otherwise stated: $s = 700$, $z = 0.5$, $N = 1000$, $\lambda = 0.3$, $\alpha = 5$, $\varepsilon = 0$, $r = 10$, $\mu = 0.1$ and $\sigma_d = 0.1$. The chosen values ensure the population does not go extinct unless mortality is higher or productivity is lower (smaller α or z) than the baseline. The main results will focus on varying α, z, ε and m; for results of variation in λ and r, as well as those where kin competition has been removed, see supplement IV).

Results

Based on the APP (Clark 1994) one might expect that breeders, being the only type of individual with 'assets', should evolve lower dispersal rates than non-breeders. We found this to be true only in a qualified way: breeders in good territories were always reluctant to disperse (Figures 1-3). In the absence of territory quality variation (Figure 1a at $\alpha = 1$), or when individuals were unable to assess the quality of their territory (Figure 3c), all breeders behaved identically, and breeding dispersal remained low as compared to juvenile dispersal. Outside these special conditions, breeders in possession of poor quality territories showed a much wider variety of responses: breeding dispersal rates could either increase or decrease with habitat quality variation (Figure1) or with the proportion of habitat that is better than their own (Figure 2). The breeding dispersal of such individuals could then either fall below or exceed that of juveniles (Figures 1-3).



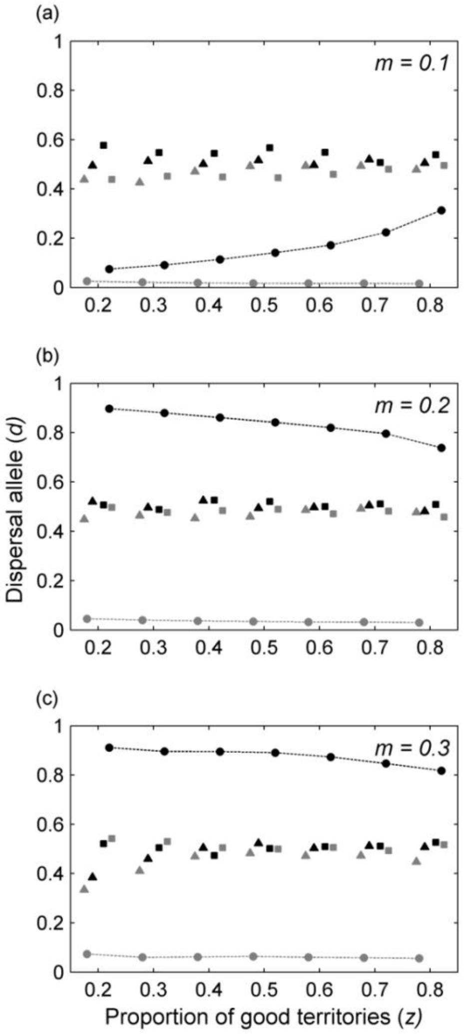


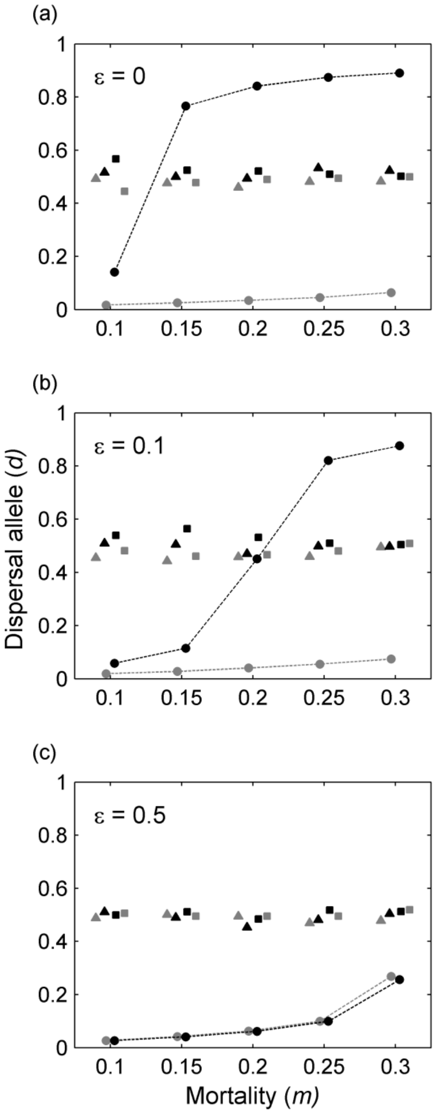
Figure 1 (Left). Evolved means of the dispersal allele with different benefits of a good territory (α) for each of the six states measured at 5000 generations for mortalities (a) $m = 0.1$, (b) $m = 0.2$, (c) $m = 0.3$. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in grey are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Note that extinctions occur in (b) and (c) with $\alpha < 3$ and $\alpha < 5$, respectively. Standard errors not shown as all S.E. < 0.02. Parameter values: $s = 700$, $z = 0.5$, $N = 1000$, $\lambda = 0.3$, $\varepsilon = 0$, $r = 10$, $\mu = 0.1$ and $\sigma_d = 0.1$.

Figure 2 (Right). Evolved means of the dispersal allele with different proportions of good territories (z) for each of the six states measured at 5000 generations for (a) $m = 0.1$, (b) $m = 0.2$ and (c) $m = 0.3$. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in grey are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Note that extinctions occur in (c) with $z \leq 0.3$. Standard errors not shown as all S.E. < 0.02 (except when extinctions occur). Parameter values: $s = 700$, $N = 1000$, $\lambda = 0.3$, $\alpha = 5$, $\varepsilon = 0$, $r = 10$, $\mu = 0.1$ and $\sigma_d = 0.1$.

The decisive factor explaining these patterns is a demographic one: breeding dispersal from poor territories increased sharply with mortality (*m*; Figure 3), though less so in the presence of large perceptual error hampering territory quality assessment (ε; as noted above, high ε creates conditions where all breeders behave similarly). These effects did not remain minor. When mortality was high and cues of territory quality were reliable, breeders in poor territories evolved much higher dispersal rates than any other type of individual (Figure 3a-b).

The explanation for such high breeding dispersal rates from poor territories highlights the pitfalls of only considering concrete possessions, such as territories, as assets. A non-breeder in our model has an invisible asset: the ability to compete for a larger number of vacancies than the one territory that a breeder is committed to. Therefore, if territory vacancies created by mortality occur at a sufficiently high rate, a non-breeder's reproductive value can exceed that of a breeder whose territory is poor. This argument fails, however, under conditions of low mortality: breeders that disperse become non-breeders and have to compete with a very large accumulated pool of non-breeders, and the high number of competitors (Figure 4) then makes it much less likely that breeding dispersal pays off at either habitat quality (Figure 3 with low *m*).

Because of these complexities, it is not obvious whether making outside options more lucrative selects for more dispersal. One way to increase the 'lucrativeness' is to increase α, the difference between reproductive success in good vs. poor sites. High α means that breeders at poor territories forego potentially much better options elsewhere, but any dispersal-promoting effect of α only occurs at low mortality (Figure 1a). Higher mortality rates negate the effect of α because they make dispersal from poor territories high throughout a large range of habitat quality variation (Figure 1b-c). The dispersal-promoting effect of *z*, the proportion of territories that are of high quality, is likewise not uniform. While it is therefore not sufficient to only consider the existence of outside options, since the likelihood of acquiring them after leaving the current option depends on the severity of competition. This competition is likely strong if there are many dispersers from other sites, and/or in case of low breeder turnover resulting from low mortality.



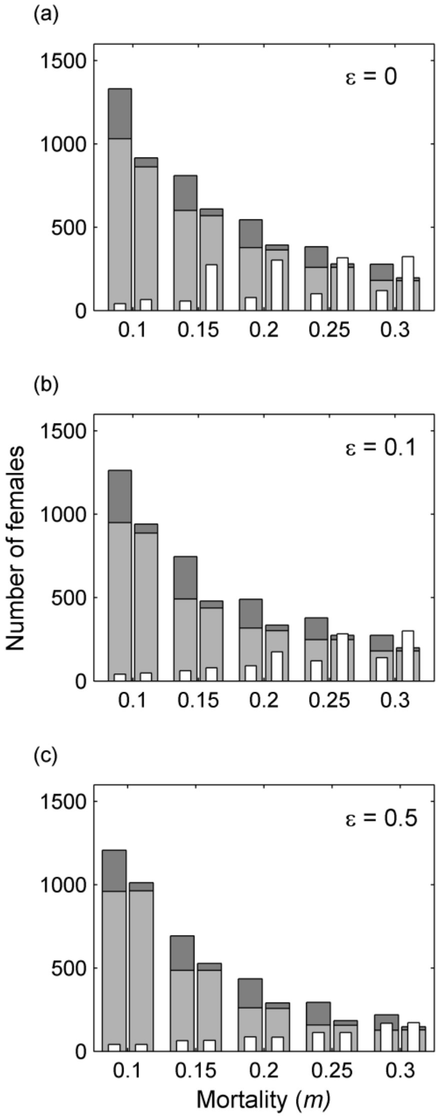


Figure 3 (Left). Evolved means of the dispersal allele with different mortality probabilities for each of the six states measured at 5000 generations for (a) no perceptual error, ε = 0, (b) ε = 0.1, (c) ε = 0.5. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in grey are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Standard errors not shown as all S.E. < 0.02. Parameter values: $s = 700$, $z = 0.5$, $N = 1000$, $\lambda = 0.3$, $\alpha = 5$, $r = 10$, $\mu = 0.1$ and $\sigma_d = 0.1$.

Figure 4 (Right). The number of non-breeding females (paired grey bars, dark grey – natal females, light grey – floater females) competing for available breeding spots (paired white bars), the left bar of each pair denotes good territories and the right bar denotes poor territories, (a) ε = 0, (b) ε = 0.1, (c) ε = 0.5. Each bar gives the mean of 40 simulations at 5000 generations. Parameter values are as in Figure 3. Note that the figure would look identical if we used males instead of females.

For non-breeders the expectations are likewise complex. On the one hand, one can extend the APP to the ‘invisible’ assets of likely future prospects in the current habitat. We would then expect non-breeders in good territories to evolve lower dispersal rates compared with non-breeders in poor territories. On the other hand, with a strong ME we would expect individuals that have already moved at least once (floaters) to evolve higher dispersal rates than non-breeding natals that have remained in their natal site. This is because information from the ME only applies in the natal territory, as we assumed no spatial autocorrelation in territory quality.

Non-breeders appear to follow the extended form of the APP, as long as relatively accurate information on habitat quality was available (Figure 3); however, differences between different categories of non-breeders were always slight (Figures 1-3). Still, especially when good territories are scarce, the dispersal rate for non-breeders from good territories is consistently lower than from poor territories (Figure 2).

It is considerably harder to detect effects of the ME, as natal individuals did not evolve systematically lower dispersal rates than floaters (Figures 1-3). Additionally, variation in reproductive success between good and poor territories does not consistently select against dispersal as the ME might predict (Figure 1). This is likely to reflect the fact that ME in its purest form assumes no knowledge beyond the emergent information that arises from demography (individuals are disproportionately born in good sites) and evolution (which impacts dispersal rates of competitors); our results show that dispersal strategies can strongly react to individuals differing in their state, particularly of the perceived habitat quality when this is possible to assess. Another fact that makes the effects of the ME harder to detect in our results is density dependence often overriding the habitat quality advantages offered by the ME. Competition for high quality breeding territories intensifies as soon as the numerous natal individuals attempt staying there (Figure 4). This means that their success of acquiring the territory becomes density-dependent: more philopatry means smaller chances of acquiring the local high quality territory. A disperser trades off these prospects for less intense competition in (potentially) poor territories, and dispersal rates evolve to be intermediate where these effects balance.

We ran a series of supplementary simulations to examine the generality of the results. Higher values of breeding success, λ, led to little change from our baseline values for all other dispersal rates than those of breeders in poor sites, which become reduced when λ is high (Figure S1). Increasing the importance of local competition (such that non-breeders compete most efficiently for a vacancy in their current territory; high r) led to little change except for a clearer differentiation between non-breeders (natals and floaters) in good vs.

poor sites (Figure S2); this makes intuitive sense because being a non-breeder at a poor site becomes more strongly penalized when most breeding vacancies are filled by a strictly local – as opposed to neighbouring – individual. Finally, when we remove kin competition from our model, the results are near identical to our original results (compare Figure S3-5 to Figure 1-3).

Discussion

Our model sheds light on why juveniles of many animals exhibit higher dispersal propensities than adults. The short answer is that the model confirms the importance of the asymmetry that an adult might already own a breeding site, which could be lost when moving; in some cases this creates situations where breeders at any site evolve low dispersal rates. However, our modelling also reveals that the caveats are important. Individuals who at first sight do not appear to own anything may be in a better position to vie for available vacancies than individuals who have settled for a less than ideal option. In the presence of habitat quality variation, we can therefore sometimes expect breeders residing in suboptimal territories to be more prone to disperse than any other type of individual. Although we have not explicitly modelled preferential treatment of individuals that reside among kin or queues of territory inheritance, such processes could further tilt the balance between philopatry and dispersal in favor of the former (see Ekman et al. 2001).

In general, our work highlights that the balance of dispersal-promoting and philopatry-promoting factors can very strongly depend both on how accurately individuals perceive their current options relative to what is available in the population as a whole (Switzer 1993; Boulinier and Danchin 1997; Schjørring 2002; Doligez et al. 2003; Valone 2007). These factors are, in our model at least, stronger than the effects of kin competition (see below). Consider, for example, the situation where accurate information of habitat quality is completely unavailable ($\varepsilon = 0.5$ in Figure 3c); now breeding dispersal remains low regardless of other parameter values. This might appear surprising, as the opposite effect — more dispersal with less information — has been found in models that make differing assumptions about information use (Enfjäll and Leimar 2009). Our result becomes intuitive, however, once one realizes that individuals that dispersed from a territory perceived to be poor would more often than half the time (if $z = 0.5$, more individuals as a whole will be born in good than poor habitat) make the mistake of leaving the state with the best reproductive value of all.

Our results also highlight the capacity of demographic parameters (here mortality) to change the rank order of dispersal propensities. Such a strong effect may appear surprising, given that mortality was identical (set at m) for every individual in the population: at first sight one might expect less breeding dispersal, not more, if the current breeding attempt is more likely to be an individual's last one, as is the case when m is high (Ronce et al. 1998, 2000). However, high mortality also means that there are few competitors alive to compete for each vacancy that is created, and this greatly improves the likely payoff of the dispersing strategy. This strengthens the view that effects of the disperser's lifespan cannot be considered in isolation from the rate of territory acquisition (see Kokko and Lundberg 2001).

There is an intriguing possibility not included in our model: the perceptual errors themselves might depend on the experience that individuals have accumulated. If breeders are more knowledgeable than floaters, our results suggest that it is not *a priori* clear that their site fidelity will increase. That is because knowing that one's own site is poor can select for leaving that site. One simple way to learn is to use one's own breeding success as a cue of habitat quality (Pärt and Gustafsson 1989; Switzer 1993; Haas 1998; Öst et al. 2011), but more detailed knowledge accumulation is obviously possible too. In this context it is interesting to note that learning has a greater scope to operate in species that are long lived enough to have time to correct their mistakes. In a habitat choice context, each mistake can take up a significant 'chunk' of lifespan (Kokko and Sutherland 2001).

Our model did not consider density-dependent dispersal strategies in the sense of individuals measuring and using local density as a cue. It is known that the consequent rules for dispersal plasticity can depend on whether dispersal is performed at the natal or adult stage (Parvinen et al. 2012), however, in these models the timing of dispersal is considered as separate scenarios rather than letting them potentially co-occur in a population. The latter type of approach would help understand when we expect either or both to occur in a specific population.

Kin competition is generally known to select for dispersal (Hamilton and May 1977; Ronce et al. 2000; Rodrigues and Johnstone 2014), yet strong effects of kin competition are not necessarily universal: e.g. in the model of Poehtke et al. 2007, a marked effect of kin competition was restricted to cases where dispersal rates remained low (< 0.1). In our model, non-breeders evolved higher rates than 0.1 based on demographic considerations alone. At least three features of our model create conditions where the selective pressure to disperse more, based on reducing the intensity of competition as experienced by related individuals at the natal site, will be relatively low. First, the most likely future breeders at the natal site are always the disperser's own parents: they retain the priority to breed at the site if they themselves do not disperse (or die). This likelihood is independent of the focal offspring's dispersal decisions. Second, high dispersal — which in our model arises through other factors — implies a continual influx of immigrants to any site, thus one disperser's efforts to reduce competition at the natal site can become relatively insignificant. Third, it should be noted that the relatedness structure in a diploid species with stochastically variable lifespans of parents (as in our model) creates less strict kin competition than in some classic models of dispersal (e.g. Hamilton and May 1977), which assumed asexual reproduction such that individuals are bound to compete with their clones.

Numerous models have confirmed that spatial heterogeneity may favor dispersal if it is conditionally expressed (e.g. McPeek and Holt 1992; Leturque and Rousset 2002; Rodrigues and Johnstone 2014). Our model is in line with this work as it, too, highlights that dispersal can be strongly shaped by heterogeneity, but as our modelling of the APP necessitates taking into account conditional (state-dependent) responses, it is probably not surprising that dispersal does not increase uniformly with the degree of heterogeneity. The habitats are at their most diverse in our model when α is high and when $z = 0.5$, but these values do not maximize dispersal. Instead, the results show how strongly demography shapes the outcomes. One might, for example, expect that high z (implying that most sites are good) select for high dispersal from the few remaining poor sites, as randomly landing at a site is likely to lead to improved site quality. However, high z also means high global productivity, and thus a disperser from a poor (or any) site faces reduced chances of acquiring a territory at all. Whether the balance then favours more or less dispersal from poor sites (Figure 2), is modulated by overall mortality, which has a strong impact on the strength of competition (Figure 4).

Although the results from our model are in many ways in agreement with established empirical knowledge — for instance, natal dispersal is more frequent than breeding dispersal in many species (Greenwood and Harvey 1982; Paradis et al. 1998; Johst and Brandl 1999), and breeding animals in good quality territories have been found to be less prone to disperse or disperse shorter distances than individuals in poorer habitats (Krebs 1971; Stacey and Ligon 1987; Cline et al. 2013) — the details of the fit between model predictions and reality remain unknown. Qualitative support, however, can be found in certain studies, in the sense that previous breeding success has been shown to lead to higher site fidelity (Haas 1998; Danchin and Cam 2002) and breeding failure as a result from e.g. predation has been show to increases the propensity and distance of dispersal even in relatively site tenacious animals (Öst et al. 2011); some species show evidence of paying attention to both intrinsic site quality and own breeding success (Kokko et al. 2004). Such results imply that breeders can be sensitive to current site quality, and indeed a key qualitative prediction from our model is that conditional dispersal rates can evolve to be much more variable among breeders than among any other class or between classes of individuals. In our model, we did not specify exactly how animals might assess site quality: we simply assumed that they do so either perfectly, or with some error. Responses that are at least partly based on own experience (see Switzer 1993) could potentially strengthen the conditionality among breeders even more, as they gather direct experience of local habitats in a manner that can be more difficult for non-breeders (though cases of public information could make such differences milder again, see Danchin et al. 2004).

Like all models, ours is a simplification of reality and the robustness of its conclusions needs to be evaluated against its assumption structure. For example, we do not necessarily expect kin competition to always play an equally minor role as in our model; above we have outlined the reasons why this is likely to happen in our particular case. We have assumed a strict dominance hierarchy in the sense that a breeder is guaranteed some reproductive output if it survives and does not disperse, while competition among non-breeders is of a much more egalitarian nature: apart from an advantage of being ‘nearby’ (the locality factor *r*), there is no impact of age or other asymmetries among individuals. We also assumed that the sole determinant of movement-related fitness is success in competing for vacant territories (of varying quality). Obviously, if there are either immediate or delayed survival consequences of spending time as a non-breeder in different habitats, then the payoff structure will become more complicated.

In conclusion, our model demonstrates that individuals can possess both visible and invisible assets when they differ in their state of territory ownership, the likely quality of the habitat they are in, the proportion of the world that has this quality and the benefits of being in a good quality site. Demography can have a major influence on whether an individual who is already breeding should commit to its site or whether it should still consider joining the pool of dispersers: high breeder turnover selects for greater dispersal propensities as a whole, and can lead to patterns that deviate from the general expectation that natal individuals should disperse more. It is only under low turnover conditions that territories of any quality are an asset worth protecting under all circumstances.

Acknowledgements

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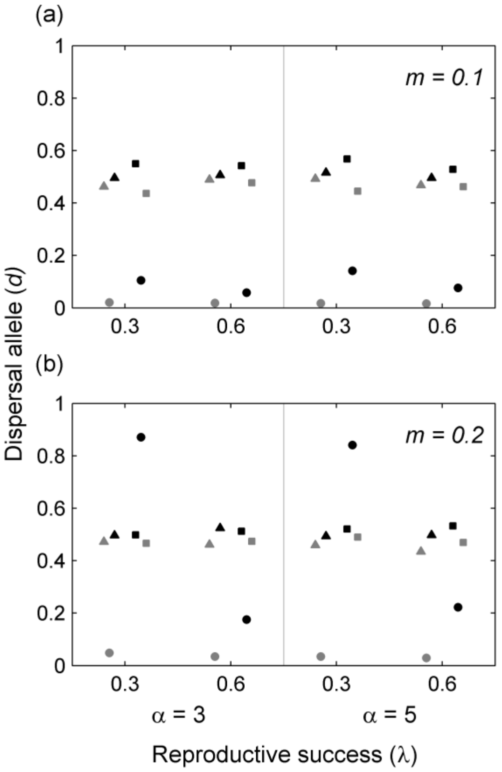
Supplement IV – Supplementary figures



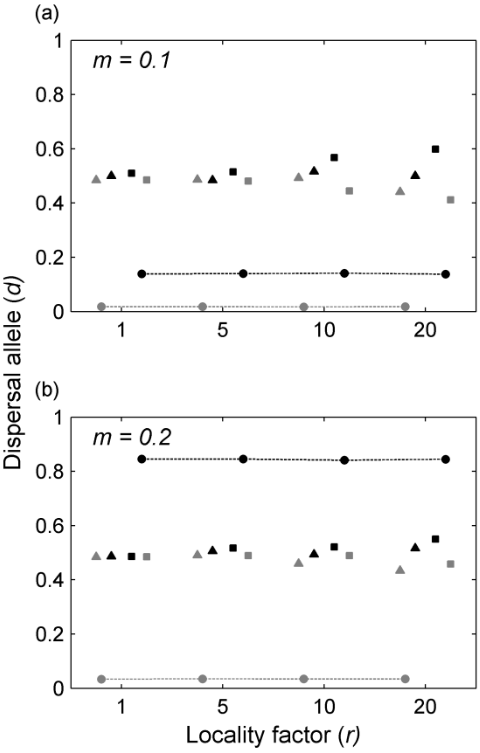
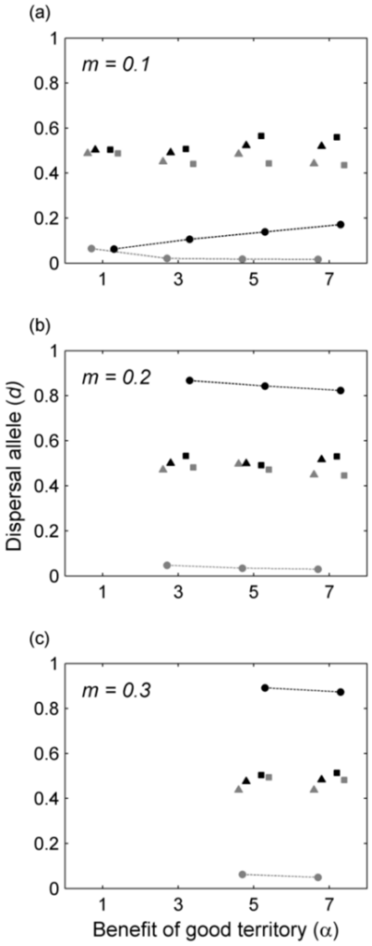


Figure S1 (Left). Evolved means of the dispersal allele with different values of reproductive success (λ) and different benefits of a good territory (α) for each of the six states measured at 5000 generations for (a) m = 0.1 and (b) m = 0.2. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in grey are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Standard errors not shown as all S.E. < 0.02. Parameter values: s = 700, z = 0.5, N = 1000, ε = 0, r = 10, μ = 0.1 and σ_d = 0.1.

Figure S2 (Right). Evolved means of the dispersal allele with different values of the locality factor value (r) for each of the six states measured at 5000 generations for (a) m = 0.1 and (b) m = 0.2. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in grey are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Standard errors not shown as all S.E. < 0.02. Parameter values: s = 700, z = 0.5, N = 1000, λ = 0.3, α = 5, ε = 0, μ = 0.1 and σ_d = 0.1.



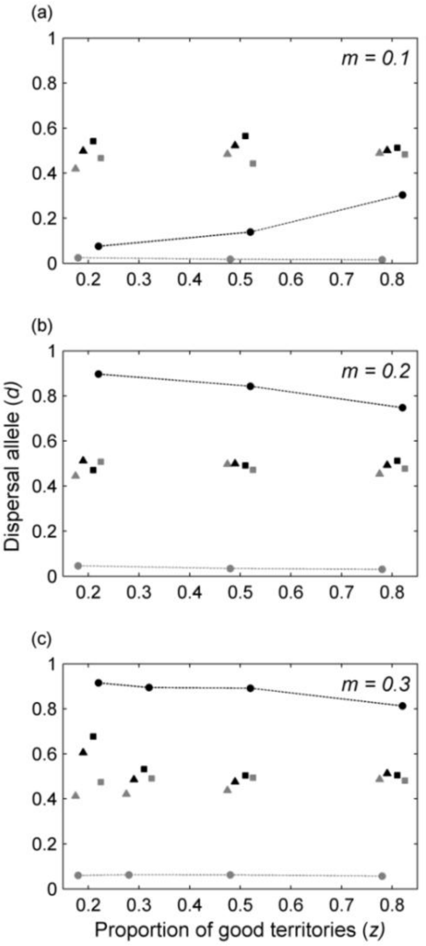


Figure S3 (Left). Evolved means of the dispersal allele without kin competition and with different benefits of a good territory (α) for each of the six states measured at 5000 generations for mortalities (a) m = 0.1, (b) m = 0.2, (c) m = 0.3. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in grey are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Note that extinctions occur in (b) and (c) with $\alpha < 3$ and $\alpha < 5$, respectively. Standard errors not shown as all S.E. < 0.02. Parameter values: s = 700, z = 0.5, N = 1000, λ = 0.3, ε = 0, r = 10, μ = 0.1 and σ_d = 0.1.

Figure S4 (Right). Evolved means of the dispersal allele without kin competition and with different proportions of good territories (z) for each of the six states measured at 5000 generations for (a) m = 0.1, (b) m = 0.2 and (c) m = 0.3. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in grey are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Note that extinctions occur in (c) with $z \leq 0.3$ in all but one of the simulations, for this reason z = 0.3 is shown. Standard errors not shown as all S.E. < 0.02 (except when extinctions occur). Parameter values: s = 700, N = 1000, λ = 0.3, α = 5, ε = 0, r = 10, μ = 0.1 and σ_d = 0.1.

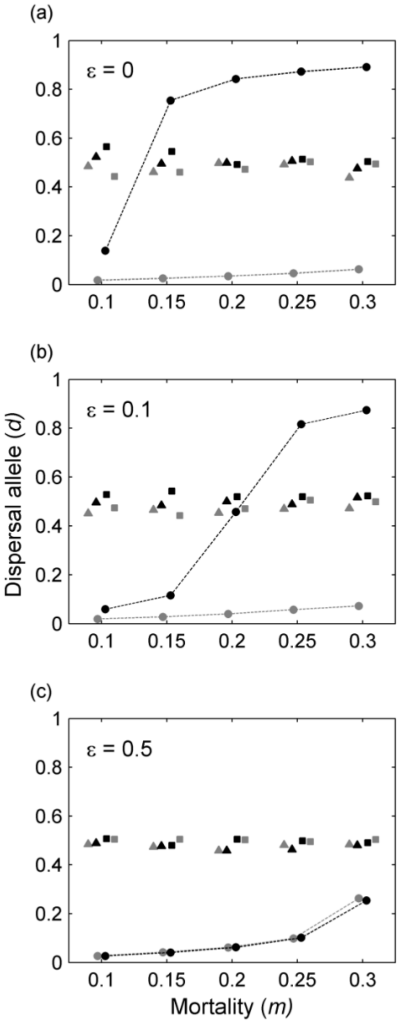


Figure S5. Evolved means of the dispersal allele without kin competition and with different mortality probabilities for each of the six states measured at 5000 generations for (a) no perceptual error, ε = 0, (b) ε = 0.1, (c) ε = 0.5. Each symbol (sometimes slightly horizontally shifted for visual clarity) gives the mean of 40 simulation runs. Symbols in grey are dispersal probabilities used by individuals in good territories, symbols in black are for poor territories. Circles connected by lines denote breeders, squares denote floaters, and triangles denote natals. Standard errors not shown as all S.E. < 0.02. Parameter values: s = 700, z = 0.5, N = 1000, λ = 0.3, α = 5, r = 10, μ = 0.1 and σ_d = 0.1.

Chapter 4 – Predation selects for later and more synchronous arrival times in migrating species.

Anna MF Harts, Nadiah P Kristensen and Hanna Kokko

Submitted to ***Oikos***

Abstract

For migratory species, the timing of arrival at breeding grounds is an important determinant of fitness. Too early arrival at the breeding ground is associated with various costs, and we focus on one understudied cost: that migrants can experience a higher risk of predation if arriving earlier than the bulk of the breeding population. We show, using both a semi-analytic and simulation model, that predation can select for later arrival. This is because of safety in numbers: predation risk becomes diluted if many other individuals, either con- or heterospecific, are already residing in the area. Predation risk dilution can also select for more synchronous arrival because deviating from the current population-wide norm to earlier or later dates leads to higher predation risk or to failures in territory acquisition, respectively. The fact that selection for high arrival synchrony can in some cases be more important than selection for a specific date (early or late) within the season is an example of an 'evolutionary priority effect': whichever strategy — in this case a particular arrival time — becomes established in a population can remain stable over long periods of time; there are many possible equilibria (multiple stable states) which the population can remain at. Mixed arrival strategies are also possible under some circumstances.

Introduction

In migratory species, the date of arrival to the breeding grounds is a key biological event that has received increasing interest in the recent literature, both as a case-study of life-history evolution (Alerstam et al. 2003) and due to its response to climate change and its role as an indicator of warming (Pulido 2007). Arrival date is known to be the result of a trade-off between multiple selection pressures. Early arrival is often beneficial in terms of male competition for territories and females (e.g. Kokko 1999; Morbey and Ydenberg 2001; Smith and Moore 2005), female competition for breeding locations (Kokko et al. 2006), reproductive success (e.g. Bensch and Hasselquist 1991; Hasselquist 1998; Teder 2014), egg-resource gathering (Nager 2006; Descamps et al. 2011; Kristensen et al. 2015), and to guarantee temporal synchrony between nestling needs and resource phenology (e.g. Both et al. 2006; Jonzén et al. 2007). However, early arrival also incurs costs if it exposes arriving individuals to harsh early-season conditions; escaping such conditions is the primary reason why migration occurs at all, thus part-time exposure to these costs can be detrimental (Newton 2008; McKinnon et al. 2010).

Predation at the breeding grounds is a significant factor affecting migratory birds (Martin 1995; Newton 1998; Fontaine and Martin 2006; Krams et al. 2014), yet the effect of predation upon adults on arrival timing has not received much attention in the migration literature (Fontaine and Martin 2006; Low et al. 2010; Chapman et al. 2011). The significance of predation for migratory populations is highlighted by findings that predation pressure can be responsible for birds selecting safer breeding sites further north (McKinnon et al. 2010), and that phenology can be affected by both the predation of adults at stop-over sites (Jonker et al. 2010; Hope et al. 2014), and nest-predation of juveniles (Borgmann et al. 2013; Du et al. 2014). However, given that predation in general is hard to measure, relatively little is known about the effects of predation on adults upon arrival at breeding grounds as a cost of early arrival (Sillett and Holmes 2002; Abrams and Ginzburg 2000; Newton 1998). The question of the effect of predation upon adults at the breeding grounds upon phenology remains therefore largely open.

Migratory species are exposed to predation risk in non-breeding areas, during migration, and in breeding areas (e.g. Sillett and Holmes 2002; Lank et al. 2003), but these risk are likely to differ for the following reason. In non-breeding areas, migrants are likely to form a smaller fraction of all potential prey than in breeding areas, at least early in the migration season. Resident predators in breeding areas, that have been sustained by those prey resources that are available throughout the year, can (partially) switch to exploiting migratory species soon after they appear. This creates an interesting dynamic for arrival times within a population of migrants, when their arrival adds a significant number of individuals to the prey community at the breeding grounds early in the spring. This creates the potential for the focal species to experience frequency-dependent predation analogous to the Darling Effect for predation upon juveniles which can select for synchronous breeding (Gochfeld 1982; Ims 1990; Langerhans 2007).

Consider (as a simplification which we will relax below) that a local bird predator takes one bird per day, and that there is an overwintering species with 50 local individuals having survived the winter. The first-arriving individual of the migratory species has mortality risk of 1/51 (assuming it is as easy for the predator to catch to catch as the resident species) if no conspecifics arrive on the same day. If it arrived one day later when

3 more conspecific individuals also arrive, it shortens the risky period by one day and now its first-day risk has been reduced to 1/(49+4) = 1/53 (note that the local community was diminished by 1 individual in the meantime). This example shows that 'safety in numbers', i.e. the predator dilution effect (Bednekoff and Lima 1998; Connell 2000; Jones 2003), can select for later arrival and potentially also for more synchronous arrival (Ims 1990). Obviously, we must also take into account that there will also be some daily mortality elsewhere than on the breeding grounds; our model below integrates across site-dependent mortality on all days of the potential arrival time period. For now, it is sufficient to note that the frequency-dependent nature of mortality risk, as described above, is probably less strong in milder conditions (the overwintering grounds) where the prey community is likely to be more diverse and abundant throughout the year.

In this study we aim to quantify the likely effects of predation upon arrival phenology by varying the likelihood of being predated in two types of models: a simulation approach where we allow for a population containing individuals with multiple different arrival time strategies, and a semi-analytical approach where we quantify the success of a mutant in an otherwise monomorphic population. Both models are based on a hypothetical migratory species in which intraspecific competition for territories yields benefits for early arriving individuals. We build our models using the biological example of migratory birds, however the results are general to any system in which the benefits of early arrival is traded against frequency-dependent selection (e.g. emergence time distribution in insects; Williams et al. 1993; Pompanon et al. 1995). In both of our models, we replace the above simplistic calculation of daily risk (above) with predation risk that is based on a Type II functional response of the predator (Murdoch 1973) when faced with two types of prey: the resident community of prey which the predator has been diminishing over the winter, and the newly arriving migrants.

Models

Simulation model

The simulation model denotes the migrating species as S1 and the resident species as S2. Note that the resident 'species' may comprise an entire community of resident animals; its precise composition does not matter for our present purpose, which is to examine the effects of predation and the availability of alternative prey on migration timing within the focal species S1.

Each S1 individual has a haploid locus δ that determines arrival time at the breeding ground within the range of options which we denote as days $T = 1 \ldots T_{\max}$. The range of δ, 0

$\leq \delta \leq 1$, is interpreted such that the lowest values correspond to arriving at the earliest possible arrival day $T = 1$, and the highest value corresponds to $T = T_{\max}$. To be precise, an individual arrives at time T whenever its δ is within the interval $\left[\frac{T-1}{T_{max}}, \frac{T}{T_{max}}\right]$. For example, if $T_{\max} = 5$, those individuals whose δ falls between 0.4 and 0.6 arrive at the breeding ground on day 3.

Selection for early arrival operates via territory quality: we assume that early arrival gives priority access to better territories. There are V territories of which a proportion α are of good quality, yielding higher reproductive success for their owners. The remaining territories are of lower quality (see below for details).

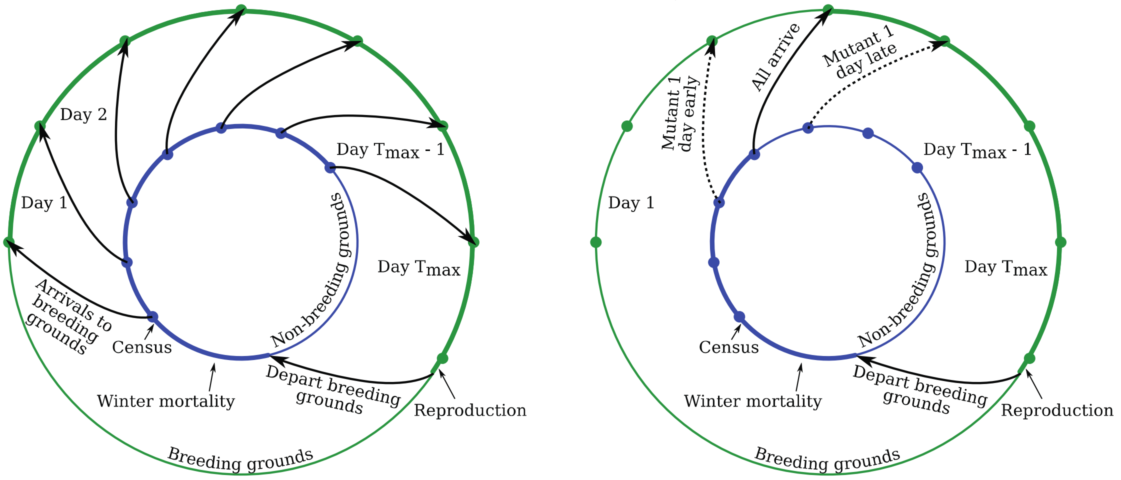
We denote total predatory effort by X, and assume that predation is the only force potentially selecting against early arrival. In reality, of course, costs of too early arrival can manifest themselves in many ways, not only through predation. We justify our choice with the conceptual clarity it produces: in the absence of predators ($X = 0$), we should see individuals arriving as early as possible, and deviations from this must be due to the effects of predation.

Each generation starts with arrival of species S1, and we track the dynamics of arrived individuals for each of the $T_{\max}$ time steps (Figure 1a). At the start of each time step those individuals arrive whose δ matches the current time, as explained above. Territory acquisition proceeds as follows for each time step T. If there are more good quality territories than individuals arriving, all individuals are assigned to a good quality territory. If there are more individuals arriving than there are good quality territories, the good quality territories will be randomly divided among the arriving individuals and the remaining individuals acquire a poor quality territory (if available). When there are more individuals arriving than there are territories, both the good and poor quality territories are randomly divided among the arrivees and the remaining individuals become floaters, i.e. they are at the breeding ground but have no territory. A floater can become a territory owner in a subsequent time step as territories become available due to predation, in which case floaters compete with arriving individuals for available territories. They acquire territories with equal probability to newly-arrived individuals. When $T = T_{\max}$, territories that have become available due to predation will be filled by randomly chosen floaters. Some territories remain without an owner if there are fewer floaters than available territories at $T = T_{\max}$.

Each time step T exposes individuals that have arrived on the breeding grounds to predation (Figure 1c). Predation occurs according to a Type II functional response with two different types of prey items (Murdoch 1973). This means that at each time step T, the number of S1 and S2 prey items taken depend on the number of individuals alive at the breeding grounds, denoted $N_1(T)$ and $N_2(T)$ respectively. Daily predation on S1 is assumed to affect floaters and territory owners equally. The number of individuals of species S2 at the beginning of the season, $T = 1$, is assumed to be constant, denoted N_2*(i.e. $N_2(1) = N_2$*). Individuals of S1 that are not yet on the breeding grounds also experience a daily mortality risk (p_0).

(a) Dynamics over 1 year, full simulation

(b) Dynamics over 1 year, semi-analytic simplification



(c) Dynamics over 1 day

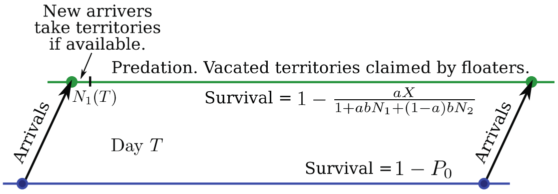


Figure 1. Diagram representing (a) the simulation model and (b) the semi-analytic simplification, (c) shows the daily arrival dynamics at the breeding ground for species S1. Starting after the census, individuals in the simulation model depart from the overwintering grounds (in blue) and migrate to the breeding ground (in green) on the day determined by their arrival time allele (δ). In the semi-analytical model the vast majority of the population arrives on day T except mutants who arrive a day earlier or later (where possible). Both models incorporate a daily mortality throughout the arrival time period, with survival probabilities shown in (c) both for individuals that have not arrived yet (above the blue line) and for individuals that have (below the green line). After arrival of all individuals, reproduction occurs in both (a) and (b), after which all individuals of species S1 migrate back to the overwintering ground where they face winter mortality before they repeat the cycle.

A Type II functional response specifies the number of individuals predated on a given day: for species S1 this is $P_1(T) = \frac{aN_1(T)X}{1+abN_1(T)+(1-a)bN_2(T)}$ and for S2, $P_2(T) = \frac{(1-a)N_1(T)X}{1+abN_1(T)+(1-a)bN_2(T)}$ (Murdoch 1973). Here a ($0 \leq a \leq 1$) is the predator preference for S1 over S2 (e.g. one species might be easier to catch than the other), such that $a = 0.5$ indicates no preference, and $a > 0.5$ indicates a preference for S1. X reflects total predatory effort, and it is proportional to predator abundance and the time they spend foraging. The handling time b includes both time spent finding and handling prey.

The interpretation of $P_1(T)$ and $P_2(T)$ is problematic for non-integer values: if we always rounded to the nearest integer to determine the number of individuals taken, then low daily predation pressures would lead to consistent rounding down to zero and the predator never eats. Therefore the fractional portion of P is treated probabilistically, e.g. $P_1 = 0.3$ means that no S1 prey are taken in 70% of cases and one prey in 30% of cases, and $P_1 = 2.9$ means that two prey are taken in 10% of cases and three prey in 90% of cases. The individuals of S1 that are predated are randomly selected from all individuals, i.e. territory owners as well as floaters, that have arrived on the breeding ground. For S2, the number of individuals that are predated are simply deducted from the current numbers (using the same rounding rules as for S1): $N_2(T+1) = N_2(T) - P_2(T)$. Not yet arrived S1 individuals are assumed to have a daily mortality risk p_0 that is applied independently for each such individual (Figure 1c).

We repeat the above procedure for each day $T = 1$ to $T_{\max}$, and then the breeding season commences. Reproductive success on a given territory is Poisson-distributed with mean R_G for good territories and R_P in poor territories ($R_G > R_P$). Offspring inherit the arrival time locus δ from their parent (i.e. asexual reproduction), but this allele may mutate in offspring with probability μ. When mutation occurs, offspring δ is changed by a value taken from an uniform distribution with range $[-\sigma, \sigma]$ (if the new value is below 0 or above 1, the new value is set to 0 or 1, respectively). The reproduction of species S2 is not tracked explicitly as we assume no significant interactions with S1 outside the period of interest (the shared predator's effects during the spring migration).

After reproduction all S1 individuals migrate, vacating all territories. Before the start of the new spring migration season each individual dies with probability γ, irrespective of the value of δ. Individuals that survive, i.e. parents and their offspring, form the $N_1(1)$ of the next spring migration season, leading to overlapping generations.

Each simulation is initiated with a specified $N_1(1) = N_1^*$ individuals of species S1 at the start of the *first* generation (and N_2 individuals of S2 as in the beginning of every spring season). The arrival time locus δ is initially normally distributed with mean ε and interval $[\varepsilon - \theta, \varepsilon + \theta]$. The simulations were run for 5000 generations. The results are shown as the average of 10 randomly chosen replicates. Parameter values used (unless varied): $a = 0.5$, $X = 850$, $N1^* = N_2^* = 1000$, $T_{\max} = 5$, $\varepsilon = 0.5$, $\theta = 0.5$, $\mu = 0.1$, $\sigma = 0.01$, $p_0 = 0.05$, $\gamma = 0.1$, $V = 500$, $b = 5$, $\alpha = 0.5$, $R_G = 2$, $R_P = 1$.

Semi-analytic model

The semi-analytic model simplifies the individual-based simulation model by assuming a monomorphic population (Figure 1b), i.e. one in which all individuals arrive to the breeding grounds on the same day. We are interested in finding out which days (between T and $T_{\max}$) are evolutionarily stable, depending on variation in predation pressure.

As we are interested in exploring the microevolutionary dynamics of the system, we use three simplifying assumptions commonly invoked in eco-evolutionary models (Geritz et al. 1998). First, we assume that the microevolutionary timescale is longer than the population dynamic timescale, such that the population can be assumed to be at population-dynamic equilibrium. Second, we assume that the initial number of mutant individuals is small enough that their effect on the dynamics and fitness of individuals in the population using the prevailing arrival strategy can be ignored. Third, we assume that the mutations themselves are small, such that we need only consider the fitness of mutant arrival day strategies that are either one day earlier or one day later than the prevailing strategy.

As in the simulation model, the daily population dynamics for the alternative-prey species during the predation and territory-allocation period is described by

$$N_2(T,\hat{T}) = \begin{cases} N_2^*, & \text{if } T = 1. \\ N_2(T-1,\hat{T})\left(1 - \frac{(1-a)X}{1+abN_1(T-1,\hat{T})+(1-a)bN_2(T-1,\hat{T}),}\right), & \text{otherwise.} \end{cases} \qquad (1)$$

where $N_1^*(\hat{T})$ is the species' population size evaluated at steady-state (which depends upon the prevailing arrival-day strategy), in accordance with our first assumption. For the focal species, the dynamics are described by

$$N_1(T,\hat{T}) = \begin{cases} 0, & \text{if } T < \hat{T}. \\ (1-p_0)^{\hat{T}-1} N_1^*(\hat{T}), & \text{if } T = \hat{T}. \\ N_1(T-1,\hat{T})\left(1 - \frac{aX}{1+abN_1(T-1,\hat{T})+(1-a)bN_2(T-1,\hat{T})}\right), & \text{otherwise.} \end{cases} \qquad (2)$$

At the end of the predation and territory-allocation period, the number of individuals remaining to reproduce is

$$M_1^*(\hat{T}) = N_1(T_{max}, \hat{T})\left(1 - \frac{aX}{1+abD_1(T_{max},\hat{T})+(1-a)bD_2(T_{max},\hat{T})}\right). \tag{3}$$

The yearly population dynamics can then be described by

$$N_1^*(\hat{T}) = (1-\gamma)\left(M_1^*(\hat{T}) + M_G R_G + M_P R_P\right), \tag{4}$$

where M_G (M_P) is the number of individuals holding a good (poor) territory at the end of the predation and territory-allocation period. $N_1^*(\hat{T})$ and $M_1^*(\hat{T})$ can be obtained numerically solving Equation 4 for different prevailing arrival-day strategies $\hat{T}$ (see data accessibility). We are interested in the scenario in which territory competition is a strong selective force and the population contains floaters, and so for the parameter range explored the population is only viable when there is complete occupancy of both types of territories, therefore M_G equals the number of good territories V_G, and likewise $M_P = V_P$.

The invasion fitness of the mutant with arrival-day strategy T' entering a population with prevailing arrival-day strategy is $\hat{T}$ is

$$W(T',\hat{T}) = (1-\gamma)p_s(T',\hat{T})\left(1 + p_G(T',\hat{T})R_G + p_P(T',\hat{T})R_P\right), \tag{5}$$

where $p_s(T',\hat{T})$ is the mutant's probability of survival, and $p_G(T',\hat{T})$ $\left(p_P(T',\hat{T})\right)$ is the probability that the mutant will obtain a good (poor) territory. In accordance with the second assumption, the mutant at invasion has no influence upon the fitness of individuals in the population using the prevailing strategy, and so their fitness is $W(\hat{T},\hat{T}) = 1$, and the mutant can successfully invade if its invasion fitness is $W(T',\hat{T}) > 1$.

The probability of an individual surviving a given day T is

$$s(T,\hat{T}) = \begin{cases} 1 - P_0, & \text{if not yet arrived at breeding grounds.} \\ \max\left(0, 1 - \frac{aX}{1+abN_1(T,\hat{T})+(1-a)bN_2(T,\hat{T})}\right), & \text{if at breeding grounds.} \end{cases} \tag{6}$$

In accordance with the third assumption, we need only consider mutants with arrival-day strategies one day earlier or one day later than the prevailing strategy.

The mutant's survival probability is the same as the prevailing strategy modified by the one more and one fewer days spent at or away from the breeding grounds. Therefore, for the mutant arriving one day earlier than the prevailing strategy

$$p_s(\hat{T}-1,\hat{T}) = \frac{M^*(\hat{T})}{N_1^*(\hat{T})} \frac{\max\left(0, 1 - \frac{aX}{1+(1-a)bN_2(\hat{T}-1,\hat{T})}\right)}{1-P_0}, \tag{7}$$

and for the mutant arriving one day later than the prevailing strategy

$$p_s(\hat{T}+1,\hat{T}) = \frac{M^*(\hat{T})}{N_1^*(\hat{T})} \frac{1-P_0}{1 - \frac{aX}{1+abN_1(\hat{T},\hat{T})+(1-a)bN_2(\hat{T},\hat{T})}}. \tag{8}$$

The mutant's probability of acquiring a good territory, a poor territory, or no territory at all, depends upon whether it arrives earlier or later. Mutants arriving one day earlier than the prevailing strategy can easily take a good territory, therefore

$$p_G(\hat{T}-1,\hat{T}) = 1\,, \tag{9a}$$

$$p_P(\hat{T}-1,\hat{T}) = 0\,, \tag{9b}$$

For mutants arriving one day later than the prevailing strategy, their probability of acquiring a good territory is equivalent to that of the prevailing strategy minus the probability of acquiring a good territory by the end of the first day

$$p_G(\hat{T}+1,\hat{T}) = \frac{V_G}{M_1^*(\hat{T})} - \frac{V_G}{N_1(\hat{T}+1,\hat{T})} = \frac{V_G(N_1(\hat{T}+1,\hat{T}) - M_1^*(\hat{T}))}{M_1^*(\hat{T})N_1(\hat{T}+1,\hat{T})}\,. \tag{10}$$

Similarly the probability of acquiring a poor territory is

$$p_B(\hat{T}+1,\hat{T}) = \frac{V_B(N_1(\hat{T}+1,\hat{T}) - M_1^*(\hat{T}))}{M_1^*(\hat{T})N_1(\hat{T}+1,\hat{T})}\,. \tag{11}$$

The invasibility of each prevailing strategy ($\hat{T}$) can now be classified according to its invasibility to mutants arriving one day earlier and one day later than the prevailing strategy (Equation 5). For example, if $W(\hat{T}+1,\hat{T}) > 1$ then the population is invasible to mutants arriving one day later. The evolutionary singular strategy (ESS) T^* is the prevailing strategy which is invasible to neither strategy

$$W(T^*-1,T^*), W(T^*+1,T^*) < 1\,. \tag{12}$$

Results

Our results confirm the intuitive expectation that the arrival time strategy evolves to be as early as possible in the absence of predation pressure (as we included no other costs of early arrival). In the simulation model, 10 replicate simulations with $X = 0$ produced the result that 6773.3 (29.7 SE) individuals arrive on day $T = 1$, while 3.4 (0.4 SE) individuals arrive on day $T = 2$, and none on days $T = 3 – 5$ (parameter values: $a = 0.5$, $N1^* = N_2^* = 1000$, $T_{\max} = 5$, $\varepsilon = 0.5$, $\theta = 0.5$, $\mu = 0.1$, $\sigma = 0.01$, $p_0 = 0.05$, $\gamma = 0.1$, $V = 500$, $b = 5$, $\alpha = 0.5$, $R_G = 2$, $R_P = 1$). The small number of individuals arriving on day two are due to mutations in the arrival allele rather than later arrival being favored by selection. In the semi-analytic model, in the absence of predation pressure we obtain a similar result. No strategy is invasible to a later arrival-day strategy ($W(\hat{T}+1,\hat{T}) = (1-\gamma)(1-p_0)^{\hat{T}} < 1$ for all $0 < p_0 \leq 1$ and $0 < \gamma \leq 1$), and for the default parameter values, $W(\hat{T}-1,\hat{T}) = (1-\gamma)(1-p_0)^{\hat{T}-2}(1+B_G) > 1$ for all $1 < \hat{T} \leq T_{max}$. Therefore all arrival-day strategies after the first day are invasible to a strategy of arrival one day earlier.

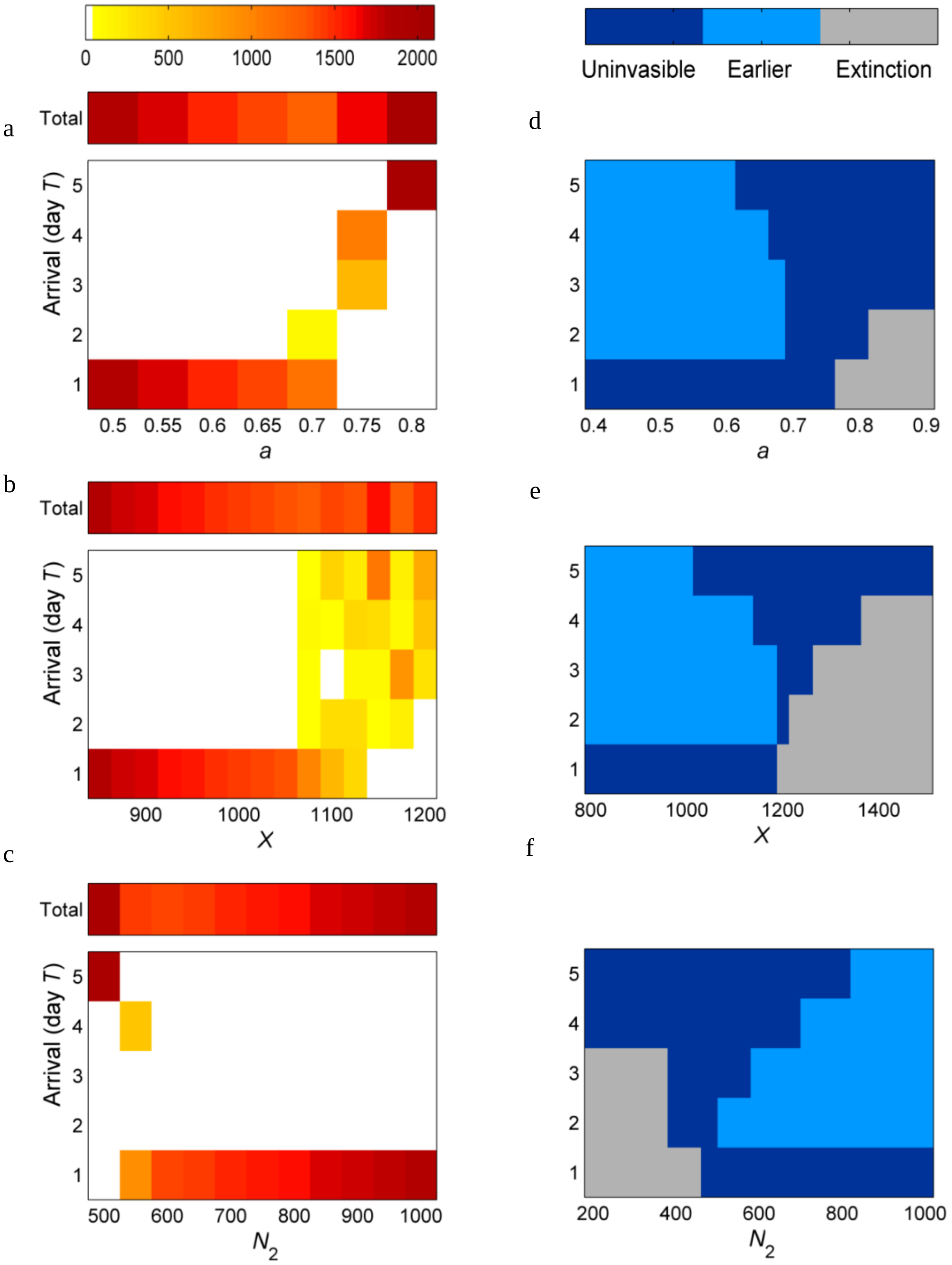


Figure 2. Evolutionary stable arrival day for two different models, the simulation model (a – c) and the semi-analytical model (d – f). Different values for *a* are shown in (a, d), for *X* (b, e), for N_2 (c, g). In (a – c), coloured (non-white) areas indicate that individuals arrive on this arrival day, the color (also see legend) indicates the number of individuals arriving (averaged over 10 simulations unless extinctions occurred), and 'total' refers to the sum of individuals alive when the census (Figure 1) is taken. In (d – f), the dark blue color indicates an ESS, light blue indicates that individuals arriving earlier have higher fitness and grey shows that extinctions occur. Note that the x-axis may span a different range for the semi-analytical model than for the simulation model. Where not specifically varied (on the respective *x* axis), we used parameter values $a = 0.5$, $X = 850$, $N1^* = N_2^* = 1000$, $T_{max} = 5$, $\varepsilon = 0.5$, $\theta = 0.5$, $\mu = 0.1$, $\sigma = 0.01$, $p_0 = 0.05$, $\gamma = 0.1$, $V = 500$, $b = 5$, $\alpha = 0.5$, $R_G = 2$, $R_P = 1$.

Figure 2a-c summarises the effect of increasing predation pressure in the individual based simulation model. Predation pressure can be increased in various ways: by increasing predator preference for the focal species a, by increasing the total predation effort X, and by decreasing the number of alternative prey N_2. In each case, we chose a baseline parameter value which leads to arriving as early as possible being favoured, and then examined the effect of stronger predation. Mild increases in the predation pressure from the baseline do not lead to a deviation from the earliest possible arrival, and the only effect is a population size decline (Figure 2a-c). Increasing the predation pressure further results in later arrival times and larger population sizes (provided the populations survive, see below).

In some simulations, when predation pressure was high ($a > 0.75$, $X > 1175$, $N_2 < 550$), some populations go extinct. This occurs when the simulations are seeded with an initial arrival strategy distribution that is unviable (initial arrival strategy: $\varepsilon = 0.5$, $\theta = 0.5$, $\delta = [0 , 1]$). It can be interpreted as a failure to undergo evolutionary rescue, where the speed of evolution was too slow compared to the loss of individuals caused by the high predation pressure. This corresponds to a scenario in which a new predator invades or an existing predator has a sudden density increase.

In all parameter value explorations, we found parameter regions where different runs of simulations did not converge to the same arrival day strategies; they retained their differences regardless of how long the simulation is run (a = 0.7-0.8, X = 1000-1200, N_2 = 500-550). The semi-analytic model (Figure 2d-f) reveals why this occurs. When predation pressure is low, the earliest arrival-day strategy is the only ESS, and it is also an evolutionary attractor: all later arrival-day strategies are invasible to the strategy of arriving one day earlier (light blue region, Figure 2d-f). However as predation pressure is increased, late arrival-day strategies emerge as alternative ESSs (dark blue region, Figure 2d-f), emerging first on the last day and then at progressively earlier days. The first late-arrival ESS to emerge is on the last day because this is where the alternative-prey (S2) populations are lowest and consequently daily predation pressure is highest. As predation pressure is increased, earlier late-arrival ESSs emerge. These late-arrival day ESSs are not evolutionary attractors, a population strategy near a late-arrival ESS will either move away from it and towards earliest arrival if it is in the light blue region of Figure 2d-f, or remain where it is if it itself is a late-arrival ESS (dark blue region). Consequently any population initiated with a strategy within the dark blue region will remain at that strategy (an ‘evolutionary priority effect’ *sensu* Gourbière and Menu 2009). Finally, when predation pressure is very strong (high a, high X, and low N_2), the earliest arrival-day strategies are no longer viable, and a population adopting such a strategy will go extinct (grey regions, Figure 2d-f).

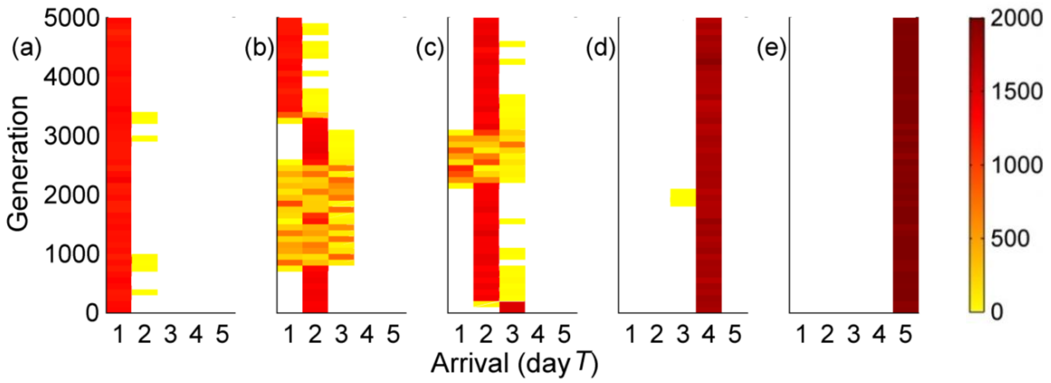


Figure 3 a – e. Simulations with a = 0.7 and different initial intervals (i.e. θ = 0.1) for the arrival allele (δ) over time, (a) initial arrival on day 1, δ = [0 , 0.2], ε = 0.1, (b) initial arrival on day 2, δ = [0.2 , 0.4] , ε = 0.3, (c) initial arrival on day 3, δ = [0.4 , 0.6] , ε = 0.5, (d) initial arrival on day 4, δ = [0.6 , 0.8] , ε = 0.7 and (b) initial arrival on day 5, δ = [0.8 , 1.0] , ε = 0.9. All other parameter values as in Figure 2. Color indicates the number of individuals arriving (see legend).

Which ESS the simulation model reaches depends upon the initial conditions and stochastic events during the evolutionary process. When simulations in the parameter range of multiple ESSs were seeded with different initial arrival day strategies, the evolutionary simulations led to different arrival day strategies. Provided that the evolutionary parameters were set such that the genetic variability was low (i.e. θ = 0.1), these evolutionary endpoints were similar to that with which they were initialised (Figure 3). This shows that alternative stable states are also possible in the simulation model, with significant inertia that constrains arrival dates to largely stay where they were initiated.

In the region for which the semi-analytic model predicted multiple ESSs, the simulation model additionally predicted that, for a given simulation, persistent mixed arrival-day strategies may occur. For example, when 10 simulations of 10,000 generations were run with X = 1125, more than half of the simulations showed the persistence of populations with a mixture of strategies although, after 10,000 generations, first or last day arrival was more common than arrival on intermediate days (Figure 4). In simulations where mixed strategies persist for a long period of time (i.e. >1000 generations), a bimodal pattern (e.g. arrival on day T =2 and day T =4) is common, suggesting that one part of the population specialises in a strategy favouring higher reproduction at the cost of higher mortality due to predation, whereas the other specialises in lower mortality at the cost of reproduction.

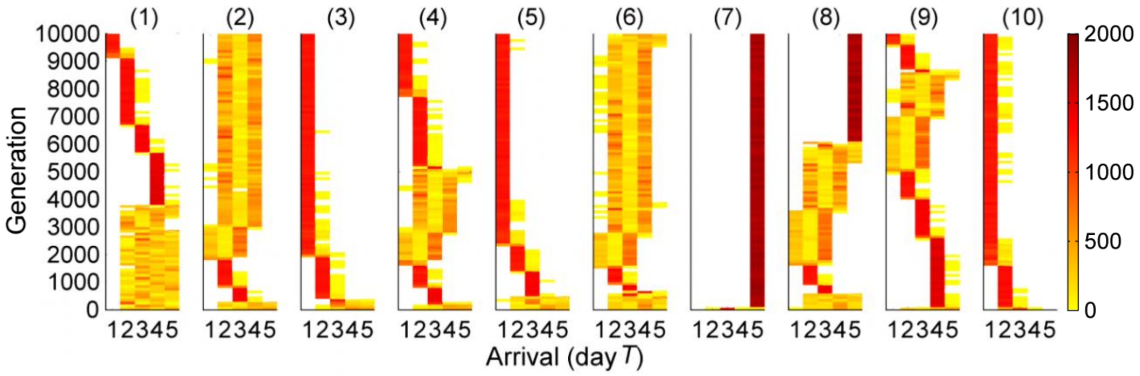


Figure 4 (1) – (10). The evolution of the arrival time allele for ten individual simulations with X = 1125, all other variables have the standard values as given with Figure 2.

Discussion

We have explored models of arrival time evolution under two competing objectives: arriving early to obtain a high quality territory versus arriving late to reduce predation risk. Our models were designed to test the idea that frequency-dependent predation can select against early arrival, but they revealed a richer set of outcomes than a simple shift towards later arrival with increased predation. Due to the frequency-dependence and the interplay of the selective forces, high predation pressure is predicted to select for synchronous arrival with conspecifics, however stochastic effects and large arrival strategy mutations can lead to persistence of populations with mixed arrival-day strategies. We discuss these below.

The importance of arriving synchronously is seen most clearly in the semi-analytic model (Figure 2d-f), where the scenario modelled is a monomorphic population, with a separation between the population-dynamic and evolutionary time-scales, and where mutations in arrival strategy are small (no greater than one day). Selection for synchronous arrival is also responsible for the finding of the individual-based simulation model that initial arrival dates can be largely retained for a very large number of generations (Figure 3). This type of 'evolutionary priority effect', where the strategy that establishes itself first can persist on an evolutionary timescale, has been discussed before in a different context of dormancy evolution (Gourbière and Menu 2009). To understand these effects in the current context, it is important to consider both (1) selection against arriving earlier than the prevailing arrival strategy and (2) selection against arriving later than the prevailing arrival strategy. We consider these in turn.

First, selection against earlier arrival can be understood as a result of predator satiation (Ims 1990) or the predator dilution effect (Bednekoff and Lima 1998; Connell 2000; Jones

2003). Predation risk, from the perspective of the prey, is frequency-dependent: individuals can reduce their predation risk by only being present at the breeding grounds when many other individuals are also present. In this way they avoid being temporarily one of only few prey items available for resident predators. When predation pressure is high, the predator dilution/ satiation effect is the dominant effect on predation risk, therefore there is strong selection against arriving earlier than the prevailing arrival strategy.

Second, selection against later arrival can be understood as the result of competition for territories. Assuming that territory acquisition is a quick process (Beletsky and Orians 1987; Smith and Moore 2003) with strict priority effects (Newton 2008 and references therein) and a limiting number of territories, the probability of acquiring a (high-quality) territory is much lower for individuals arriving even one day after the prevailing arrival-day strategy. To understand why, consider the extreme case where most individuals arrive synchronously on the same day. On this day all territories are vacant and available to the competing individuals. In contrast, after this day the only territories that are available to competing floaters and late-arrivers are those that have been vacated due to a territory-holder being predated. Compared to this cost of much lower territory acquisition, the benefits of arriving one day later than the prevailing strategy are meagre: they consist of a small reduction of predation risk compared to individuals using the prevailing strategy, i.e. a difference of one day exposure to predation.

The net effect of selection against both earlier arrival and later arrival above is that the population cannot be invaded by either strategy, and hence synchronous arrival remains evolutionarily stable. It is noteworthy that the models predict that many adjacent days can all be alternative ESSs. Selection for synchrony means that, to avoid predation, it is best to arrive when the majority does so, regardless of other timing issues. Earlier would be dangerous, while later would mean losing out in the competition for territories. This implies, in accordance with the evolutionary priority effect, that there may be a certain degree of 'inertia' in arrival times: it is costly to deviate from the norm if the norm brings about advantages in terms of predator dilution effect. This result has implications for climate change scenarios, where phenological adaptation to a shift in nestling food resource phenology may be hindered by the stabilising selection for phenological synchrony caused by predation pressure.

Our prediction of synchronous arrival date for migratory birds in response to frequency-dependent adult predation is analogous to breeding synchrony in other systems. For example, the evolution of emergence time of juvenile salmon is a trade-off between predation risk and territory acquisition; early emergers miss out on dilution effects resulting in heavy mortality from predation, but late emergers suffer from habitat saturation and have difficulty finding high quality feeding habitats (Cutts et al. 1999). As other examples, the mast fruiting of plants, the synchronous emergence of 13-year periodical cicadas, and synchronous metamorphosis in toads may have all evolved to take advantage of predator satiation (Gochfeld 1982; Williams et al. 1993; Devito et al. 1998). Finally, both spatial clustering and temporal breeding synchrony have been observed in many bird taxa (Danchin 1988; Ims 1990; Rolland et al. 1998; Varela et al. 2007). Known as the Fraser Darling effect, it is a strategy of using nest-predator satiation to reduce individual predation risk (Nisbet 1975; Ims 1990; Langerhans 2007). To our knowledge, ours is the first study to suggest that a similar effect may also affect adult migratory phenology.

When the individual-based simulation model is run with genetic parameters set such that genetic variability is high, the model predicts the persistence of populations of mixed arrival day strategies. This difference in results between the simulation and semi-analytic model is due to the different scenarios that are implied by their assumptions. In the simulation model the population has (at least initially) variation for the arrival allele while the semi-analytic model assumes a monomorphic population for the arrival time allele. The invasion approach of the semi-analytic model assumes that there are few individuals that arrive earlier or later than the general population, and only one day earlier or later than the general population, and tests whether these 'invaders' have higher fitness than the general population. In contrast, the simulation model permits many invaders to arrive at once, and potentially invaders whose arrival strategy is more than one day different to the prevailing strategy.

Which model is most suitable depends upon the particulars of the system of interest. Typically eco-evolutionary phenology models use analytic techniques that make similar assumptions to the semi-analytic model here (e.g. Jonzén et al. 2007; Kristensen et al. 2015), however full individual-based simulations are able to reveal much more complex dynamics than can be deduced from analytic techniques alone.

The effects of predation upon arrival for migratory species appear understudied, as research has largely focussed on predation during migration or during nesting (e.g. Lindström 1990; Sillett and Holmes 2002; Fontaine and Martin 2006; Chapman et al. 2011; Sofaer et al. 2013). This is largely due to the difficulty of distinguishing between predation and movement to other breeding locations before egg laying (Sillett and Holmes 2002; Alerstam et al. 2003). One reason why predation upon pre-breeding adults may have received less attention is that it has a limited effect upon population persistence. In populations with many floaters, any territory holder that dies can be rapidly replaced, and so predation of adults at the pre-breeding stage will not usually reduce the number of offspring produced (Newton 1998); this is also true in our model. However, we have shown that predation at this crucial time of the life cycle can influence arrival time phenology very significantly despite the small number of individuals affected: precisely because the local population remains small early in the season, the per capita risk can remain significant. The consequent evolutionary response may in turn influence synchrony between peak nestling resource demand and resource phenology. In such cases, predation will influence offspring numbers indirectly, and the predicted inertia could have a stronger impact still if climate change shifts the nestling-resource's phenology.

We note a number of simplifications in both models. Firstly, we assumed that the predator's relative preference for the migrant species is constant across all migrant densities (i.e. we assume Type II rather than more complicated functional responses). Perhaps more importantly, our models ignore interyearly fluctuations in weather, food availability, and predator and alternative prey abundances. These have been shown to impact traits such as breeding success (e.g. Sofaer et al. 2013) and selection could consequently fluctuate more in time than in our model. Weather may also make it likely that migrant species find it in practice difficult to reach as high synchrony as predicted by our model (unless they travel physically together, as many migrants do; our model together with flocking advantages during travel might give a good set of reasons why individuals strive to keep together during the journey).

In conclusion, our models suggest that the combination of competition for limited breeding territories and strong frequency-dependent predation will select for not only later arrival times but also for more synchronous arrival times, with stochasticity in arrival strategy also potentially leading to the persistence of populations of mixed arrival-day strategies. This dual prediction was made possible by the fact that we explored both a full individual-based simulation as well as a more traditional semi-analytic model that uses the adaptive dynamics framework. This result is made possible by taking a game-theoretic approach to the role that synchronicity with conspecifics plays in predator evasion via the predator satiation effect.

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Chapter 5 – Mate-guarding and frequent copulation in birds: a meta-analysis of their relationship to paternity, male quality and male parental care.

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Abstract

In many bird species males are presumed to protect their paternity by guarding their mate intensely or by copulating frequently. These costly behaviours are assumed to reduce sperm competition and thereby elevate paternity. In recent decades much has been written about sperm competition and extra- and within-pair paternity in birds. However, we lack a recent meta- or comparative analysis on behaviours that are assumed to protect a male's paternity. Here we conduct a meta-analysis to address three key questions related to correlates of presumed paternity protection. First, we simply ask if mate-guarding and/or frequent copulation are positively associated with a male's paternity. Second, we test the predictions of a frequently proposed hypothesis, which is based on the premise that females should prefer a high quality male to sire offspring because of his 'good genes'. For socially monogamous species this implies that a female is unlikely to seek extra-pair matings if her social male is of high quality. High quality males should therefore less often perform behaviours that protect their paternity, and we thus ask if there is evidence for such a pattern. Third, we focus on the relationship between paternal care and paternity protection. Paternal care is costly so, all else being equal, we expected that cuckolded males will provide less care. But how do males know whether there are unrelated offspring in their nest? We test whether the intensity with which a male protects his paternity acts as a proxy for certainty of paternity and thereby generates a positive correlation between paternity protection behaviour and the level of male paternal care. Our results indicate that (1) presumed paternity protection behaviours are significantly positively correlated, albeit weakly, with paternity ($r = 0.18$) and that (2) males of higher quality use presumed paternity protection behaviours significantly less often ($r = -0.19$). However, closer inspections shows that this pattern only holds for mate-guarding ($r = -0.28$), and not for frequent copulation which is (non-significantly, P=0.057) positively correlated with male quality ($r = 0.33$). We also find that (3) males that invest more in

presumed paternity protection behaviours tend to provide more care ($r = 0.23$, although this trend is marginally non-significant, $P = 0.056$). We combine our results with existing knowledge to provide an overview of the relationships between paternity, paternity protection, parental care, male quality and other relevant factors in birds.

Introduction

Behaviours presumed to protect paternity are important male traits that have likely evolved because they increase net male reproductive success (Parker 1970; Alcock 1994). In birds, it is assumed that males commonly use mate-guarding and/or frequent copulation to protect their paternity (Møller and Birkhead 1991). Depending on the species' mating system and life history, males may use one or both of these types of putative paternity protection. Mate-guarding by males can be described as a behaviour in which a male remains close to his pair-bonded female to deter extra-pair copulation attempts. Mate-guarding behaviours include the male following the female's movements and spending a large proportion of the time within a short distance of her (Birkhead and Møller 1992). For example, during the fertile period male bluethroats (*Luscinia s. svecica*) stay a larger proportion of their time in close proximity to their mate, and the male also follows the female far more often during this period than when she is no longer fertile (Krokene et al. 1996). Mate guarding appears to ensure that a male can interfere with, or even prevent, other males' copulation attempts (Westneat 1994; Currie et al. 1999). In birds, mate-guarding occurs predominantly post-copulation during the female's fertile period. The fertile period is thought to be from around 5 to 10 days before the first egg is laid, until the day the penultimate egg is laid (Birkhead and Møller 1992). Mate-guarding is often observed to be most intense from approximately 4 or 5 days before the first egg is laid until, depending on clutch size, the day the first egg is laid, or one or two days after the first egg is laid (e.g. Krokene et al. 1996; Foerster and Kempenaers 2005; Hoi et al. 2011). Many bird species that use mate-guarding also copulate far more often than seems necessary for fertilization alone (Hunter et al. 1993; e.g. Hoi et al. 2011).

Frequent copulation is often the sole type of putative paternity protection in bird species where males are unable to guard their mates, e.g. due to the simultaneous need for long feeding trips and nest defence (Møller and Birkhead 1991). During the fertile period these within-pair copulations are more frequent (e.g. Barber and Robertson 2007; Hoi et al. 2011), although there are examples of species where males have also been observed to copulate frequently with their mate before the fertile period (e.g. Villaroel et al. 1998). In tree swallows (*Tachycineta bicolor*) frequent copulation during the presumed fertile period involves approximately 18 copulation attempts per hour, and approximately 5 of these attempts per hour are expected to be successful (defined as leading to cloacal contact), resulting in an average of 322 copulation attempts during the presumed fertile period (Crowe et al. 2009).

The purpose of paternity protection is to avoid or reduce sperm competition and reduce extra-pair paternity. Sperm competition has received a lot of interest over the last few decades (e.g. Parker 1970, Birkhead and Møller 1998; Jennions and Petrie 2000; Simmons 2001; Alonzo and Pizzari 2013); so too has within and extra-pair paternity, since the discovery of affordable DNA techniques to assign parentage (Griffith et al. 2002). This has led to a number of hypotheses — some adaptive, others mechanistic or proximate — that offer explanations for variation in levels of extra-pair paternity between species, populations and among individual males (Westneat et al. 1990; Kempenaers et al. 1992; Hasselquist et al. 1996; Petrie and Kempenaers 1998; Westneat and Stewart 2003; Neudorf 2004; Akçay and Roughgarden 2007). See Table 1 for a brief overview of the hypotheses we refer to in text (also see Forstmeier et al. 2014 for a recent overview).

Despite intense research on many of these hypotheses (see Stutchbury and Morton 1995; Westneat and Sherman 1997; Møller and Ninni 1998; Griffith et al. 2002; Matysioková and Remeš 2014; Arct et al. 2015), a crucial factor has received little attention: how paternity protection behaviours that are assumed to increase paternity relate to actual paternity. For example, there are no recent comparative analyses, meta-analyses or reviews on paternity protection in birds. A meta-analysis by Møller and Ninni (1998) is the most recent publication we are aware of that compares behaviours associated with paternity protection across species.

There is variation in the intensity with which individual males seem to protect their paternity, and for various species there have been attempts to relate putative mate guarding to a male's share of paternity (e.g. Dunn et al. 1994; Kempenaers et al. 1995; Møller and Tegelstrom 1997; Johnsen et al. 2003). Paternity protection is likely a costly behaviour (e.g. due to an associated reduction in foraging time) (Lens et al. 1997; Komdeur 2001; Low 2006) so we would only expect it to have evolved and be maintained if there are compensatory benefits. The most obvious benefit would be ensuring paternity. Here we therefore perform a meta-analysis investigating the relationship between two behaviours (mate guarding and frequent copulation) associated with paternity protection and (within-pair) paternity. In their meta-analysis Møller and Ninni (1998) reported a non-significant relationship, but since 1998 the cost and ease of detecting extra-pair paternity have resulted in many additional scientific publications on the topic, warranting an updated analysis.

Hypothesis or topic	Explanation, prediction	Ref.
Good genes	A female should seek the best genes for her offspring by mating with a high quality male, irrespective of whether this male is within- or extra-pair.	1,2,3,4
Genetic compatibility/ similarity	Females seek genes for their offspring that are compatible with their own genes, or at least not incompatible (e.g. due to mating with a related individual).	4,5,6
Other/direct benefits to female	A female may receive other benefits from extra-pair mating, for example in the form of foraging opportunities, future mating, mate replacement, additional paternal care.	7
Protect against infertility of social male	Females seek EPC's to protect against infertility of their social mate.	8,9
Mate guarding trade-off	A male has to 'choose' how he divides his time between protecting his paternity, searching for extra-pair copulations and other essential activities, e.g., feeding.	1
Male care trade-off	Males face a trade-off between caring for offspring and investing this energy in other activities, e.g. feeding or finding additional mating opportunities.	10
Female constraint	A male is expected to provide care to the offspring in response to his share of paternity or his certainty of paternity.	11
Breeding density/ short NND	Short distance to other males or females means increased opportunity for EP opportunities.	12,13
Breeding synchrony/ asynchrony	Synchronous breeding allows females to easily find EPC's. Alternatively, more asynchronous breeding can facilitate EPC's because males can protect their paternity and search for EPC's.	14
Polygyny	Polygynous males are expected to be unable to effectively protect their paternity with primary females, dependent on when the male attracts a secondary female.	1
Longevity	Long lived species have long term pair bonds and these are expected to be associated with higher fidelity.	15

Table 1. Overview of hypotheses referred to in text for different aspects of within and extra-pair paternity. References: 1) Westneat et al. 1990, 2) Jennions and Petrie 2000, 3) Mays and Hill 2004, 4) Akçay and Roughgarden 2007, 5) Brown 1997, 6) Arct et al. 2015, 7) Petrie and Kempenaers 1998, 8) Sheldon 1994, 9) Morrow et al. 2002, 10) Trivers 1972, 11) Westneat and Sargent 1996, 12) Møller and Birkhead 1993a, 13) Westneat and Stewart 2003, 14) Stutchbury and Morton 1995, 15) Mauck et al. 1999.

For most of the last two decades, the dominant assumption has been that females engage in extra-pair copulations to gain indirect, genetic benefits (e.g. Petrie and Kempenaers 1998; Jennions and Petrie 2000; Akçay and Roughgarden 2007; for a recent critique of this idea see Forstmeier et al. 2014). Based on this 'good genes' hypothesis one would generally predict that a female paired to a high quality male is less likely to search for and accept extra-pair copulations (e.g. Kempenaers et al. 1992). Does this then mean that high quality males can afford to protect their paternity less? Alternatively, it might pay for these males to invest as heavily, or more heavily, in protecting their paternity simply because they have larger energy reserves than lower quality males; this idea applies if guarding benefits everyone but varying costs are the main driver of observed effort levels. This is the classic conundrum of the extent to which variation in resource acquisition will lead to a negative phenotypic correlation between traits that *a priori* would seem to require a trade-off (Van Noordwijk and de Jong 1986). Here we document the phenotypic relationship between male quality and the two putative behavioural measures of male investment into paternity protection. Finally, because the intensity with which a male invests in protecting his paternity may be a cue as to his likely share (certainty) of paternity, we report the phenotypic relationship between the two putative measures of paternity protection and the resultant level of male paternal care. Based on the two main hypotheses involving paternal care in Table 1 the expectation would be that males that protect their paternity more intensively (i.e. are more certain of their paternity) will also provide more paternal care. Again, however, this assumes that variation in male quality does not alter the value of investing in different paths to fitness (e.g. see Kokko & Jennions 2008 for the argument that males with high mating success should decrease their parental investment; in the current context this is particularly relevant for those species, included in our analysis, where the male may be polygynous and possess several nests).

We aim to combine our results on the three relationships (paternity protection and paternity, paternity protection and male quality and paternity protection and paternal care) with existing knowledge to provide an overview of the relationships between these three factors in birds.

Methods

Literature search

The literature was searched for studies containing data on two forms of paternity protection that are common in birds, specifically, frequent copulation and mate guarding. This search was performed using ISI Web of Science and was updated until 1 January 2014. We used each of the key words ‘guard*’, ‘fertilization*’, ‘paternity’, or ‘copulation*’, within the following Web of Science categories: *Ecology, Zoology, Evolutionary Biology, Ornithology, Biology, Behavioral Sciences* and *Multidisciplinary Sciences*. Additionally, we performed a forward search on a previous meta-analysis on paternity studies by Møller and Ninni (1998) to locate and include papers that cited it. We did not attempt to find papers in other ways, or seek out unpublished datasets from colleagues, as these methods can themselves introduce biases (Murtaugh 2002, Jennions et al. 2013). Our search method resulted in 20 882 unique references after duplicates were removed.

The references returned by these searches were initially assessed based on the journal name, title and abstract (see Figure 1 for an overview of the selection process). Papers on taxa other than birds or on an irrelevant topic were excluded (for example, references on 'mammalian guard hairs'). We initially included references with information on within- or extra-pair paternity and male quality even if paternity protection was not mentioned, because it became apparent that the required data was sometimes published without it being the main focus of a paper. For inclusion in the meta-analyses a paper had to meet eight criteria.

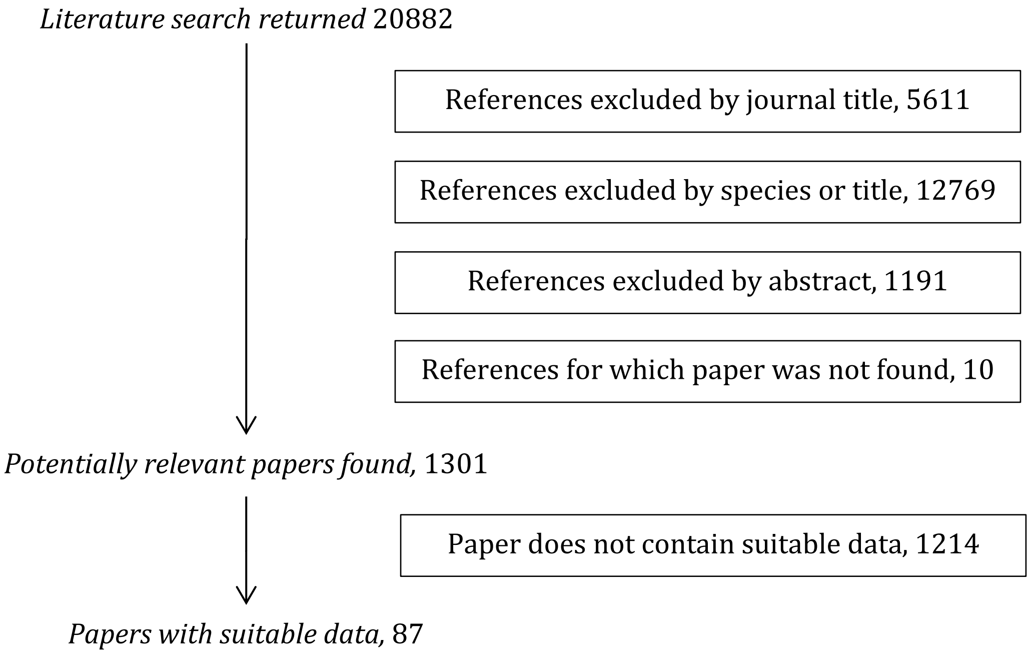

Figure 1. Flow diagram showing the paper selection process.

(1) The publication reported the relationship between paternity protection (namely frequency of within-pair copulations and/or mate guarding) and at least one of three factors (a) paternity, (b) male quality or (c) paternal care (for definitions of each factors see data extraction and coding).

(2) The data were from socially monogamous or polygynous species that form pairs at a nest. In the case of polygynous species the study had to report on the male's primary nest. Other mating systems and types of pairs were excluded (e.g. cooperative breeding, polyandry and polygamy).

(3) The study was not performed with captive birds (i.e. in an aviary or on farmed birds).

(4) The data were from a single breeding event for the population (e.g. the first breeding attempt in species with multiple clutches per season).

(5) The data were specific to the fertile period. Where possible we only used data from the peak fertile period (~4 days prior to laying the first egg until the day before the last egg was laid). If this period was unavailable we accepted data from up to 10 days prior to laying the first egg until the day before the last egg was laid.

(6) Paternity was determined by so-called 'DNA methods' (see Griffith et al. 2002).

(7) The paper contained appropriate statistics or raw data and sample sizes so that effect sizes and variances could be calculated.

(8) The calculation of paternity was based on chicks per nest rather than on a subset of the population. For example, we exclude a case where the level of extra-pair paternity was reported for the entire population per year (Korpimäki et al. 1996).

For ten references we were unable to locate the paper, but given that 87 out of 1301 papers contained suitable data (Figure 1), the likelihood that these few papers contained data that could change the outcome of our meta-analysis is very small.

Data extraction and coding

We used the Pearson correlation coefficient (r) as our measure of effect size. When a study did not report a correlation but included other statistics, the effect size (r) was calculated from the reported statistics (e.g. mean ± S.D., t, F, p, R^2) using standard formulae (see Lipsey and Wilson 2001; Nakagawa et al. 2007; Borenstein et al. 2009; Koricheva et al. 2013). Our first preference was for correlation coefficients (including Spearman rank, Kendall τ and R^2), second for raw means with standard deviations, third for a 2 x 2 frequency table, fourth for statistics in the form of t, F, U, Wald and Z, fifth by calculating the mean and standard deviation or a 2 x 2 frequency table from raw data given in the text (including from tables or graphs), and finally from p-values (p-values were first transformed to t). The correlation coefficients (r) were subsequently transformed to Fisher's Z (Z_r) for use in analyses. We did not include results that were reported only as non-significant or as "$p >$ " (e.g. "all $p > 0.3$") for a test.

In a few instances several publications reported results for a species for the same year and population. To avoid overlapping data or duplicated results we only allowed one paper to provide data for a population for a specific study period. We used the data from the paper that best matched our preference for the reported test statistic, or that was likely to include the most data.

These criteria yielded 87 papers that contributed 92 studies with 228 effect sizes for 50 species (see supplement V for this dataset). "Paper" serves as an identity for a single publication per species (with one exception, Kempenaers et al. 1998 has data on two species and, for ease of analysis, this has been given two separate paper identifiers). "Study" is used to identify independent data published within a single paper, such as data from different years or different populations. Conversely, data in separate papers from the same population in the same year, but addressing different questions or measures, were assigned the same study identity to account for their non-independence (there is only one such occurrence: Kempenaers et al. 1992 and 1995).

For each reported measure of the relationship between paternity protection and paternity or male quality or paternal care we calculated an individual effect size. We calculated separate effect sizes for different years or populations. Thus a paper could contribute multiple effect sizes for a particular relationship. Measures of paternity protection were grouped into three categories: mate guarding, copulation frequency, and manipulation of paternity protection. The measure *mate guarding* comprises measures such as the mean distance between the social pair, or the proportion of time spent together/apart. *Copulation frequency* is the observed within-pair rate of copulation. *Manipulations of paternity protection* were used in several studies. The most frequently used method was to temporarily remove a paired male or female, thereby lowering the ability of the male to guard or copulate frequently with his mate.

Depending on the study, *Paternity* was presented as within-pair and/or extra-pair paternity at the male's nest. We adjusted the sign of the measure accordingly: more within-pair or fewer extra-pair offspring in a clutch equate to higher values for paternity.

Male quality was measured in a variety of ways across and within papers, using several different traits as proxies or indicators. We grouped these different measures of male quality into the following categories: age, colour, hormone, polygyny, size or song. *Age* is a measure of male age, which was often represented as a class, because in many species it is only possible to make a distinction between young and older males. *Colour* includes different measures of colouration, such as hue and brightness, and experimental manipulations of colour or the use of colour bands that affect male attractiveness. *Hormone* is a measure of testosterone levels and includes manipulations using testosterone implants. *Polygyny* distinguishes between males that have attracted one (monogamous) or multiple (polygynous) females. *Size* includes measures of mass, measures of body or ornament size and body condition. Finally, *Song* is a measure of acoustic output by the male. In general it was clear that the authors of the original papers considered the trait in question to be a signal or correlate of male quality.

Finally, *Paternal care* comprised a male's contribution (which could be expressed relative to his mate and/or in absolute terms) to either feeding of young or the incubation of eggs.

Table 2 shows an overview of the number of papers, studies, species and effect sizes per question. The direction of the effect sizes is based on the direction of the relationship between the variables. A positive direction thus indicates that: 1) more intense paternity protection behaviours correspond to higher paternity, 2) males of higher quality perform more intense paternity protection and 3) males that protect their paternity more intensely provide more paternal care.

			# papers	# studies	# species	# ES
All			87	92	50	228
Q1 Paternity	All		46	46	32	81
	Guard		28	28	24	51
	Manipulation		12	12	11	15
	Copulation		14	14	12	15
Q2 Male quality	All		40	42	28	109
	Guard		36	38	24	97
		Age	16	16	12	26
		Color	6	8	3	18
		Hormone	2	2	2	4
		Polygyny	6	5	5	11
		Size	12	12	9	31
		Song	5	5	4	7
	Manipulation		-	-	-	-
	Copulation		11	11	10	12
		Age	1	1	1	1
		Color	1	1	1	1
		Polygyny	5	5	5	6
		Size	4	4	3	4
Q3 Parental care	All		17	18	15	38
	Guard		2	2	2	2
	Manipulation		11	11	9	27
	Copulation		5	5	5	9

Table 2. Overview of the number of papers, studies, species and effect sizes for each of the three questions for different measures of paternity protection. Male quality is divided into the different trait categories.

Our method sometimes resulted in multiple effect sizes (ES) for the same relationship from a single study. For example, a study could look at the relation between age and mate guarding intensity and use multiple measures of mate guarding (e.g. one ES for distance between social pair and another ES for time together). To handle non-independence of the data in the analysis we used two different approaches. First, we used a standard random-effects meta-analysis, which required that each study contribute a single effect size. For this we calculated a weighted mean effect size per study for each analysis (using a within-study meta-analysis). Second, we used a multi-level random-effects meta-analysis, which allowed for the use of multiple, non-independent effect sizes from a study by including the random factors 'study' and 'species' in the model. We also control for phylogenetic non-independence. The type of male quality or paternity protection was included as a fixed moderator.

We calculated the variance in Z_r as 1/(N–3), where N always refers to the number of breeding pairs included in the study. In Supplement V we also include information on four other moderators used in our analyses: species, year of publication, paper and study. For 18 effect sizes the authors did not indicate the direction of the effect (i.e. we could extract or calculate an effect size but not its direction). This was always associated with statistically non-significant results. In an attempt to control for the uncertainty introduced by these directionless effect sizes we used the following three-step approach. First, we excluded them from the analysis (dataset 1). Second, if the first analysis revealed a significant mean effect we included the directionless effect sizes but used $r = 0$ (and thus $Z_r = 0$) as the effect size (dataset 2). Third, if the analysis was still significant we assigned a direction opposite to that predicted (for Q1 and Q3 this is negative and for Q2 positive) (dataset 3).

Standard random-effects meta-analyses

Separate random-effects meta-analyses were conducted for each question. As mentioned above a study contributed one (weighted) ES to any given analysis. For each question a meta-analysis was conducted across the categories combined ('All') and then for each individual category. For example, for Q1 the 'All' analysis included effect sizes for the relationship between paternity and all measures of paternity protection: mate-guarding, manipulation of paternity protection, and copulation frequency. We then ran separate meta-analyses of the relationships between paternity and mate-guarding, paternity and manipulation of paternity protection, and paternity and copulation frequency. However, we did not run separate analyses for categories that contained fewer than four effect sizes.

We used a restricted maximum likelihood (REML) method to estimate τ^2 in all our random-effects meta-analytic models. A meta-regression was used to determine the effect of publication year for each question, separately for all categories combined ('all') and then for each category. We ran these meta-regressions separately due to the use of weighted mean effect sizes, to test for any differences among the categories of paternity protection or male quality. We used Cochran's Q statistic and I^2 to estimate the heterogeneity in effect sizes.

Multi-level (phylogenetic) random-effects meta-analyses

In the multi-level meta-analyses studies we included all effect sizes for each question by using species and study as moderators. Because this method implicitly assumes that there is no within-study correlation between effect sizes, i.e. $r = 0$ (see Booksmythe et al. In press) we also ran all the models with a correlation between effect sizes of $r = 0.5$ (see Supplement VI, Table S1 and S2 for the results). Note that the results with correlations between effect sizes are qualitatively very similar to those that do not (compare Table 6 and 7 to Table S1 and S2). We used Bayesian Markov Chain Monte Carlo (MCMC) generalised mixed-effects models to determine the overall effect size. For each of our three question we ran four multi-level models: 1) a null model, which included species and study as random effects, 2) a multi-level meta-regression, which added two moderator variables (publication year and category) to the null model, 3) a phylogenetic null model, which added information on phylogenetic relationships to the null model (i.e. model 1), and 4) a phylogenetic meta-regression, which added phylogeny to the multi-level meta-regression model (i.e. model 2). Models 2 and 4 were run without the intercept to obtain the mean estimates for the fixed effects directly. We ran models that included a phylogeny twice, using two different avian phylogenetic trees (the Ericsson tree and the Hackett tree: birdtree.org, Jetz et al. 2012; see Figures S1 and S2 in Supplement VI). In tables and figures we present the results for the Ericsson tree. The results for the Hackett tree are in Supplement VI, Tables S3-S5. The results from the two phylogenetic models were quantitatively similar, although for Question 1 they yield qualitatively different results based on the $p = 0.05$ threshold.

We used an inverse Gamma prior ($V = 0.002$ and $nu = 1$) for the random effects in all our multi-level models. The models were run for 1,100,000 iterations with a burn in of 100,000 iterations and a thinning interval of 1000. We calculated a modified version of the I^2 statistic to estimate the heterogeneity (Nakagawa and Santos 2012). We report phylogenetic heritability, H^2, as an index of the phylogenetic signal.

Publication bias

To test for publication bias we visually inspected funnel plots of the relationship between effect sizes and their precision (1/SE). Variance in the observed effect sizes should decrease with increasing sample size (as sampling error is reduced) and this pattern is expected to be symmetrical. Asymmetry in the funnel plot can indicate potential publication bias (Jennions et al. 2013). We used Egger's regression (Egger et al. 1997) to statistically test for funnel plot asymmetry. We also used the trim-and-fill method (Duval 2005) as a further test of publication bias. These tests were performed on the data excluding directionless effect sizes (i.e., dataset 1). For the multi-level meta-analyses the model residuals were used in tests of bias.

All statistical analyses for the standard random-effects meta-analyses and bias detection were conducted in R using the metafor package (Viechtbauer, 2010). For the multi-level random-effects meta-analysis we used the MCMCglmm package in R (Hadfield 2010, Hadfield and Nakagawa 2010).

Results

Standard random-effects meta-analyses

Question 1: Paternity protection and paternity

There was a significant positive relationship between factors predicted to increase paternity and a male's realized paternity when looking at all measures of paternity protection combined or when looking separately at mate guarding or manipulation of paternity protection (Figure 2A, Table 3). There was, however, no significant relationship between copulation frequency and paternity (Table 3). These findings were robust to the use of more conservative datasets (datasets 2 and 3), with the exception that the relationship between mate guarding and paternity was marginally non-significant (p = 0.057) for the most conservative data set (Table 3).

Question 2: Paternity protection and male quality

Across measures of paternity protection we found a significant negative relationship between paternity protection and male quality. Higher quality males invest less in traits that protect paternity (Table 3), although with the more conservative dataset the relationship was marginally non-significant (p = 0.053 in dataset 2, Table 3). When considering the data for mate-guarding and copulation frequency separately, there was a significant negative relationship between mate-guarding and male quality and a significant positive relationship between copulation frequency and male quality (Table 3, Figure 2B). More attractive males invest less in mate guarding, but copulate more frequently with their mates.

Question	Trait 1	Trait 2	Dataset	*k*	*m*	*n*	Mean (*r*)	L. CI	U. CI	*z* value	*p*(z)	Q	df (Q)	*p* (Q)	I^2 (%)
1	All		1	43	31	1144	0.183	0.089	0.274	3.776	0.000	74.45	42	0.001	40.54
			2	46	32	1199	0.168	0.078	0.255	3.641	0.000	76.39	45	0.002	38.15
			3	46	32	1199	0.162	0.070	0.251	3.423	0.001	79.68	45	0.001	40.60
	Guard		1	25	23	509	0.166	0.027	0.299	2.334	0.020	42.42	24	0.012	42.41
			2	28	24	564	0.134	0.010	0.253	2.117	0.034	43.28	27	0.025	35.51
			3	28	24	564	0.124	-0.004	0.249	1.903	0.057	45.78	27	0.013	39.34
	Manipulation		1	12	11	335	0.228	0.066	0.378	2.742	0.006	22.80	11	0.019	50.31
	Copulation		1	14	12	300	0.084	-0.043	0.208	1.299	0.194	13.04	13	0.445	6.06
2	All		1	36	23	1339	-0.187	-0.349	-0.013	-2.110	0.035	184.32	35	0.000	83.68
			2	42	28	1460	-0.153	-0.300	0.002	-1.938	0.053	199.19	41	0.000	81.14
	Guard	All	1	32	19	868	-0.275	-0.429	-0.105	-3.131	0.002	154.33	31	0.000	82.49
			2	38	24	976	-0.241	-0.379	-0.093	-3.152	0.002	159.51	37	0.000	78.80
			3	38	24	976	-0.211	-0.358	-0.053	-2.614	0.009	171.23	37	0.000	80.89
		Age	1	14	11	423	-0.294	-0.548	0.010	-1.901	0.057	72.43	13	0.000	88.34
		Color	1	6	1	81	-0.278	-0.487	-0.038	-2.260	0.024	1.24	5	0.941	0.00
			2	8	3	139	-0.155	-0.327	0.027	-1.673	0.094	3.55	7	0.830	0.00
		Polygyny	1	5	5	139	-0.418	-0.552	-0.263	-4.950	0.000	1.74	4	0.783	0.00
		Size	1	9	6	203	0.040	-0.284	0.357	0.237	0.813	28.91	8	0.000	76.57
		Song	1	5	4	137	-0.423	-0.705	-0.024	-2.070	0.039	17.09	4	0.002	78.71
	Copulation	All	1	11	10	296	0.334	0.115	0.523	2.930	0.003	32.91	10	0.000	70.07
		Polygyny	1	5	5	143	0.129	-0.137	0.378	0.954	0.340	8.78	4	0.067	55.25
		Size	1	4	3	83	0.414	0.006	0.705	1.986	0.047	7.42	3	0.060	63.66
3	All		1	18	15	488	0.227	-0.006	0.437	1.910	0.056	76.78	17	0.000	82.51
	Manipulation		1	11	9	310	0.347	0.036	0.596	2.174	0.030	51.65	10	0.000	85.89
	Copulation		1	5	5	107	0.173	-0.190	0.494	0.935	0.350	11.04	4	0.026	63.82

Table 3. Results from the random-effects meta-analyses for each of the questions. Paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care. Trait 1 is the category of paternity protection and trait 2 the category for male quality where applicable, *k* = the number of effect sizes, *m* = the number of species and *n* = the number of broods.

We ran seven separate meta-analyses for the relationship between measures of paternity protection and each individual 'male quality' category that had four or more effect size estimates. For mate-guarding there was a significant negative relationship for three categories: *colour, polygyny* and *song* (Figure 2B, Table 3), although the effect for *colour* was not significant with the more conservative dataset 2 (Table 3). The relationships between mate-guarding and male *size* or *age* were non-significant (Table 3). There was no significant relationship between copulation frequency and *polygyny*, while the relationship with male *size* was significantly positive (Table 3). Larger males copulate more frequently with their mates.

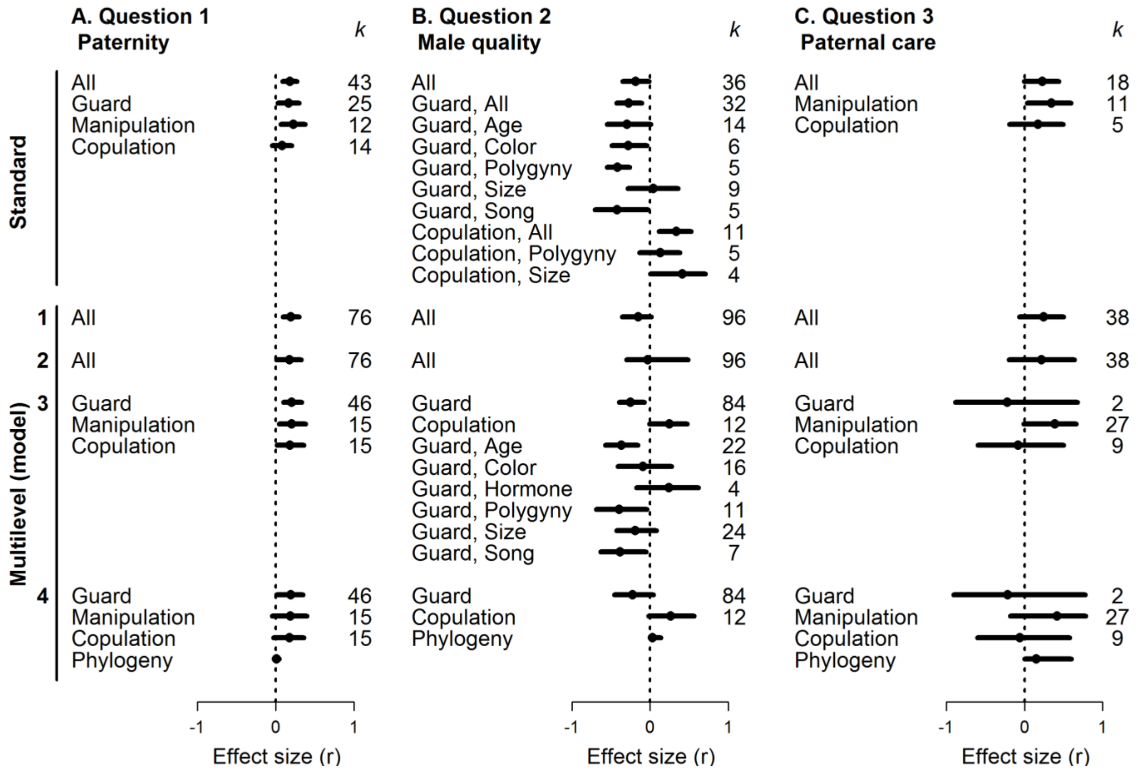

Figure 2. Forest plots of the meta-analytic means for A. Question 1, B. Question 2 and C. Question 3. 'Standard' refers to the results from the standard random-effects meta-analyses and 'Multilevel' refers to the results from the 4 models for multilevel (phylogenetic, Ericsson phylogeny) random-effects meta-analyses. See the main text for a description of the categories. *k* = the number of effect sizes.

Question 3: Paternity protection and paternal care

Combining all measures of paternity protection there was a marginally non-significant positive relationship with paternal care (p = 0.056, Table 3, Figure 2C). The trend was for males that protected their paternity more to provide greater paternal care. We ran separate meta-analyses for manipulated paternity protection and copulation frequency in relation to paternal care. We found a significant positive result for manipulations of paternity protection (Table 3), indicating that males from manipulated pairs provided less care for their offspring than control males. The relationship between copulation frequency and paternal care was non-significant (Table 3).

Heterogeneity and publication bias

The heterogeneity (I^2) in effect sizes (Table 3) was low to moderate for Question 1 and moderate to high for most of the relationships tested within Questions 2 and 3 (Table 3, Figure A3 in Supplement VI). We ran meta-regressions with year of publication as a moderator to explain some of this heterogeneity (Table 4). For Question 1 publication year explained a significant proportion of the heterogeneity for the relationship between paternity and 'all' measures of protection, and for the relationship between paternity and copulation frequency. More recently published articles had more positive effect sizes. For Question 2, publication year affected only the relationship between mate-guarding and *age* (earlier publications had smaller effect sizes) and for Question 3 publication year affected the relationships between paternal care and both copulation frequency and manipulations of paternity protection (earlier publications had more positive effect sizes).

Question	Trait 1	Trait 2	Q_1	p	$B_{[year]}$	L. CI	U. CI
1	All		7.291	0.007	0.123	0.034	0.211
	Manipulation		2.092	0.148	0.127	-0.045	0.292
	Guard		2.174	0.140	0.106	-0.035	0.241
	Copulation		5.083	0.024	0.138	0.018	0.255
2	All		0.228	0.633	-0.041	-0.209	0.128
	Guard	All	0.542	0.462	-0.064	-0.229	0.106
		Age	6.071	0.014	-0.311	-0.520	-0.066
		Color	0.358	0.550	0.135	-0.300	0.523
		Polygyny	0.587	0.444	-0.074	-0.256	0.114
		Size	0.334	0.563	0.093	-0.217	0.386
		Song	0.030	0.863	0.048	-0.461	0.533
	Copulation	All	1.967	0.161	0.158	-0.063	0.364
		Polygyny	0.248	0.618	0.088	-0.252	0.409
		Size	0.149	0.699	0.123	-0.467	0.638
3	All		2.803	0.094	-0.187	-0.388	0.032
	Manipulation		5.189	0.023	-0.327	-0.559	-0.047
	Copulation		5.545	0.019	-0.335	-0.565	-0.059

Table 4. Meta-regression results for year from the random-effects meta-analysis. Paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care. Trait 1 is the category of paternity protection and trait 2 the category for male quality where applicable, L. CI and U. CI are the lower and upper confidence intervals respectively.

Inspection of the funnel plots revealed varying levels of asymmetry in our different analyses (Figure A3 in Supplement VI). Egger's regression test indicated a publication bias for studies of the relationship between paternity and mate-guarding (Q1), and studies of the copulation frequency and *polygyny* relationship (Q2; Table 5). However, for these two potential cases of publication biases trim-and-fill did not identify 'missing studies'. Trim-and-fill did, however, identify missing studies in the following three tests addressing Question 2: mate-guarding and *age*, mate-guarding and *song*, and copulation frequency and *size*; and for two tests of Question 3: 'all' measures of protection and paternal care, and copulation frequency and paternal care (Table 5). Correcting for these 'missing studies' resulted in stronger (greater absolute magnitude) mean effect sizes but did not qualitatively alter results, except that the mean estimated relationship between 'all' measures of paternity protection and paternal care became significantly greater than zero (Table 5).

Multilevel (phylogenetic) random-effects meta-analyses

The results of the multilevel random-effects meta-analyses (Table 6) were largely in agreement with those of the standard meta-analyses (see Table 3, analyses using 'All' measures combined). For Question 1 (paternity protection and paternity), multilevel Model 1 confirmed that males that protect their paternity more have greater realized paternity (Figure 2A). For Question 2 (paternity protection and male quality) the trend for higher quality males to protect their paternity less was marginally non-significant in multilevel Model 1 (Figure 2B). For Question 3 multilevel Model 1 indicated that the relationship between paternity protection and paternal care was non-significant (Figure 2C).

Model 2 estimated the effects of different trait categories as moderators in the analysis. These can be compared to the results of the standard random-effect meta-analyses for individual categories (compare Table 7 to Table 3; Figure 2). Again, the standard and multilevel approaches mainly yielded very similar results; but for the individual categories of male quality there were some surprising differences between the two meta-analytic approaches. In contrast to the standard model, in multilevel Model 2 there was a significant relationship between mate guarding and *age*, with older males protecting their paternity less than younger males. The relationship between mate-guarding and *colour*, which was significantly negative in the standard meta-analysis, was not significant in multilevel Model 2. Because copulation frequency did not have a significant relationship with male quality we did not test individual male quality categories.

Question	Trait 1	Trait 2	*t*, *Egger's*	*Df* (t)	*p* (*t*)	*Missing k: TAF*	Mean (*r*)	L. CI	U. CI	*z* value	*p*(z)	Q	df (Q)	p (Q)	I^2 (%)
1	All		1.513	41	0.138	0									
	Manipulation		-1.115	10	0.291	0									
	Guard		2.860	23	0.009	0									
	Copulation		0.539	12	0.600	0									
2	All		0.397	34	0.694	0									
	Guard	All	-0.194	30	0.848	0									
		Age	-0.249	12	0.831	5	-0.484	-0.677	-0.228	-3.497	0.001	136.56	18	0.000	90.58
		Color	0.390	4	0.716	0									
		Polygyny	0.076	3	0.944	0									
		Size	-0.888	7	0.404	0									
		Song	2.481	3	0.089	1	-0.546	-0.804	-0.117	-2.423	0.015	27.69	5	0.000	86.51
	Copulation	All	0.297	9	0.773	0									
		Polygyny	4.528	3	0.020	0									
		Size	-0.799	2	0.508	2	0.621	0.232	0.839	2.901	0.004	18.5	5	0.002	78.31
3	All		0.583	16	0.568	5	0.380	0.163	0.563	3.322	0.001	141.64	22	0.000	86.20
	Manipulation		1.311	9	0.222	0									
	Copulation		-1.589	3	0.210	2	0.325	-0.160	0.598	1.870	0.061	16.58	6	0.011	65.81

Table 5. Results of Egger's regression tests and trim-and-fill (TAF) tests for the random-effects meta-analyses. Paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care. Trait 1 is the category of paternity protection and trait 2 the category for male quality where applicable, L. CI and U. CI are the lower and upper confidence intervals respectively.

Question	Model	Data-set	*k*	*m*	*n*	Mean (*r*)	L. CI	U. CI	I^2_{study} (%)	I^2_{species} (%)	$I^2_{\text{Effect size}}$ (%)	$I^2_{\text{phylogeny}}$ (%)	I^2_{total} (%)	H^2 (%)
1	1	1	76	31	1144	0.196	0.096	0.298	20.49	14.20	11.83		46.52	
		2	81	32	1199	0.185	0.096	0.279	23.70	12.24	9.62		45.55	
		3	81	32	1199	0.180	0.088	0.275	27.75	11.33	9.08		48.17	
	3	1	76	31	1144	0.176	0.012	0.327	17.77	11.87	10.60	10.03	50.26	23.73
		2	81	32	1199	0.166	-0.030	0.288	19.76	10.39	9.41	9.59	49.15	21.30
2	1	1	96	28	2262	-0.151	-0.354	0.015	4.75	55.53	22.53		82.81	
	3	1	96	28	2262	-0.028	-0.303	0.483	4.12	39.63	19.81	21.16	84.73	46.80
3	1	1	38	15	869	0.246	-0.065	0.498	9.40	15.75	66.40		91.55	
	3	1	38	15	869	0.219	-0.197	0.639	7.23	12.68	59.17	13.35	92.43	13.67

Table 6. Results from the multilevel meta-analyses for each of the questions, paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care, for Models 1 and 3 (null model and phylogenetic null model (Ericsson phylogeny), respectively). k = the number of effect sizes, m = the number of species and n = the number of broods. L. CI and U. CI are the lower and upper confidence intervals respectively.

Q	M	Data set	k	Paternity protection	Mean (r)	L. CI	U. CI	I^2_{study}	I^2_{species}	$I^2_{\text{Effect size}}$	I^2_{phylo}	I^2_{total}	H^2
1	2	1	46	Guard	0.205	0.098	0.334						
			15	Manipulation	0.203	0.047	0.383						
			15	Copulation	0.182	0.018	0.362						
				Year	0.086	-0.014	0.170	18.08	14.29	12.53		44.89	
		2	51	Guard	0.178	0.045	0.277						
			15	Manipulation	0.215	0.040	0.364						
			15	Copulation	0.167	-0.009	0.322						
				Year	0.082	-0.016	0.158	19.09	12.36	11.03		42.47	
		3	51	Guard	0.169	0.055	0.294						
			15	Manipulation	0.209	0.029	0.361						
			15	Copulation	0.172	-0.004	0.322						
				Year	0.076	-0.014	0.162	24.71	10.93	10.26		45.90	
	4	1	46	Guard	0.197	0.012	0.352						
			15	Manipulation	0.187	-0.045	0.399						
			15	Copulation	0.180	-0.025	0.362						
				Year	0.085	-0.013	0.170	17.47	13.96	11.93	8.66	43.37	26.09
		2	51	Guard	0.170	-0.006	0.328						
			15	Manipulation	0.199	-0.010	0.400						
			15	Copulation	0.166	-0.043	0.341						
				Year	0.079	0.002	0.180	19.53	12.16	10.20	8.08	41.88	24.09
2	2	1All	84	Guard	-0.249	-0.393	-0.074						
			12	Copulation	0.250	-0.009	0.476						
				Year	0.029	-0.086	0.140	7.55	46.01	23.93		77.49	
		2All	97	Guard	-0.239	-0.393	-0.086						
			12	Copulation	0.246	-0.007	0.461						
				Year	0.038	-0.062	0.141	7.84	50.88	17.20		75.93	
		3All	97	Guard	-0.206	-0.384	-0.030						
			12	Copulation	0.250	-0.032	0.455						
				Year	0.053	-0.066	0.157	7.73	53.16	17.91		78.80	
		1 Guard	22	Age	-0.369	-0.570	-0.155						
			16	Color	-0.092	-0.409	0.273						
			4	Hormone	0.242	-0.171	0.617						
			11	Polygyny	-0.394	-0.689	-0.039						
			24	Size	-0.189	-0.428	0.084						
			7	Song	-0.383	-0.630	-0.053						
				Year	-0.041	-0.164	0.074	4.35	59.88	12.64		76.87	
		2 Guard	26	Age	-0.358	-0.534	-0.144						
			18	Color	-0.057	-0.351	0.243						
			4	Hormone	0.244	-0.165	0.596						
			11	Polygyny	-0.378	-0.654	-0.036						
			31	Size	-0.164	-0.362	0.070						
			7	Song	-0.370	-0.611	-0.042						
				Year	-0.033	-0.161	0.084	4.12	65.85	8.25		75.23	
		3 Guard	26	Age	-0.307	-0.503	-0.053						
			18	Color	0.025	-0.275	0.349						
			4	Hormone	0.237	-0.183	0.630						
			11	Polygyny	-0.363	-0.667	0.027						
			31	Size	-0.132	-0.386	0.103						
			7	Song	-0.409	-0.636	-0.043						
				Year	-0.011	-0.126	0.113	6.84	61.78	9.78		78.39	

Q	M	Dataset	k	Paternity protection	Mean (r)	L. CI	U. CI	I^2_{study}	I^2_{species}	$I^2_{\text{Effect size}}$	I^2_{phylo}	I^2_{total}	H^2
2	4	1	84	Guard	-0.225	-0.455	0.042						
			12	Copulation	0.262	-0.016	0.561						
				Year	0.027	-0.081	0.135	8.19	44.36	24.23	10.14	76.78	50.38
3	2	1	2	Guard	-0.222	-0.886	0.679						
			27	Manipulation	0.390	-0.012	0.659						
			9	Copulation	-0.079	-0.595	0.498						
				Year	-0.238	-0.499	0.098	7.62	15.95	67.35		90.93	
	4	1	2	Guard	-0.217	-0.905	0.777						
			27	Manipulation	0.417	-0.184	0.780						
			9	Copulation	-0.060	-0.604	0.576						
				Year	-0.259	-0.531	0.080	7.04	13.04	69.79	16.04	89.88	12.48

Table 7. Results from the phylogenetic multilevel meta-analyses for each of the questions, paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care, for Models 2 and 4 (multi-level meta-regression and phylogenetic multi-level meta-regression (Ericsson phylogeny), respectively). k = the number of effect sizes, m = the number of species and n = the number of broods. L. CI and U. CI are the lower and upper confidence intervals respectively.

Question	Model	Data-set	*t, Egger's*	*Df* (t)	p (t)	*Missing k: TAF*	Mean (r)	L. CI	U. CI
1	1	1	0.938	74	0.351	0			
	3	1	0.874	74	0.385	0			
2	1	1	0.379	94	0.706	11	-0.057	-0.121	0.008
	3	1	0.360	94	0.720	11	-0.056	-0.120	0.009
3	1	1	0.560	36	0.579	0			
	3	1	0.536	36	0.593	0			

Table 8. Results of Egger's regression tests and trim-and-fill (TAF) tests for the multilevel meta-analyses. Paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care for Models 1 and 3 (null model and phylogenetic null model (Ericsson phylogeny), respectively). L. CI and U. CI are the lower and upper confidence intervals respectively.

Phylogenetic results

In general, inclusion of the phylogenies did not greatly change the model outcomes (compare Model 1 to Model 3, and Model 2 to 4; Tables 6 and 7, respectively). In some cases, where the confidence interval boundary was close to 0 for Model 1 and 2, the inclusion of a phylogeny altered the estimate so that the boundary fell on the other side of zero in Model 3 or 4.

Heterogeneity and publication bias

Table 6 shows the variance not due to sampling error for models 1 and 3 (and table 7 shows these for models 2 and 4) that can be attributed to differences between: studies (I^2_{study}), species (I^2_{species}) , and at the effect size level ($I^2_{\text{effect size}}$), and, for model 3, the variance due to the phylogeny ($I^2_{\text{phylogeny}}$). For model 3 we also measured the phylogenetic signal (H^2, Table 6 and 7), which estimates how much of the variation is explained by the phylogeny. We ran meta-regressions (Models 2 and 4) with year of publication as a moderator to see if it can explain some of this heterogeneity. Year did not explain a significant proportion of this variation for any of the three questions, with the exception of the phylogenetic meta-regression (Model 4) for Question 1 (Table 7).

Egger's regression tests based on model residuals did not suggest asymmetry in the distribution of effects for any of the multilevel meta-analyses (see funnel plots, Figure S4 in Supplement VI). Although for Question 2 trim-and-fill identified 11 missing studies on the left side in both the phylogenetic and non-phylogenetic models, adjusting our estimates to account for these putative missing studies would still not result in a mean effect that differed significantly from zero (Table 8). Trim-and-fill did not identify 'missing studies' in any of the models for Questions 1 or 3.

Discussion

The results of the two types of random-effects meta-analyses (standard and multilevel) used here are always in agreement for direction, even though on some occasions one type reported a significant effect while the other type suggested a marginally non-significant effect. We will discuss the patterns for each question separately based on the general consensus from the different models. For the exact significance level associated with specific models see the Results section.

Do the presumed paternity protection behaviours predict paternity?

The first obvious question about putative paternity protection behaviours is whether they actually protect a male's paternity. Our results suggest that they do, although perhaps only weakly (mean $r = 0.18$; 'All'). When we look at the individual categories of presumed paternity protection, both mate-guarding ($r = 0.17$) and manipulations of paternity protection (e.g. male removal, $r = 0.23$) are positively correlated with paternity. The relationship between frequent copulation and paternity is, however, non-significant. A previous meta-analysis reported that the relationship between mate-guarding or copulation frequency and actual paternity was non-significant (Møller and Ninni 1998).

The larger sample size, hence greater statistical power, available for our analysis is likely to be one factor responsible for the significant results we obtained.

It is possible, however, that the number of actual studies conducted is even larger still, but that some results remain unpublished due to their statistical non-significance (the file drawer problem, Rosenthal 1979). This concern is partly substantiated by our observation that some of the studies used in our meta-analysis reported the results of the relationship between paternity protection and paternity as 'additional results', i.e. paternity protection was not the main focus (e.g. Bjørnstad and Lifjeld 1997; Lifjeld et al. 1998; Buchanan and Catchpole 2000). It is also worth noting that we included studies that measured paternity and putative paternity protection behaviours even if they did not detect any extra-pair paternity in the population (e.g. Mota and Hoi-Leitner 2003).

Paternity protection behaviours are seemingly costly: this idea underlies the expectation that a positive relationship with paternity is expected to offset these costs. Mate-guarding is costly in terms of energy expenditure, risk of injury, reduced feeding opportunities and greater predation risk (Birkhead and Møller 1992; Komdeur 2001; Cooper and Vitt 2002; Low 2006; Ancona et al. 2010; Rodríguez-Muñoz et al. 2011). Similarly, frequent copulations are likely to be energetically costly (Birkhead and Møller 1992; Lens et al. 1997), may reduce the vigilance of pair members (Hunter et al. 1993) and increase the risk that sexually transmitted diseases or microbes are transferred (Lombardo et al. 1996; Stewart and Rambo 2000, though the risks are presumably smaller when frequently copulating with the same partner than dividing the copulations among multiple ones).

Although, as already outlined, we might expect that the effort a male puts into paternity protection should relate to his actual paternity, it is worth noting that a male's share of paternity is also strongly dependent on female cooperation (Birkhead and Møller 1993; Lifjeld et al. 1994; Petrie and Kempenaers 1998). Female control of paternity can arise in the form of, for example, active pursuit and timing of extra-pair copulations (EPCs) by females or sperm ejection after mating (Birkhead and Møller 1993; Lifjeld et al. 1994; Pizzari and Birkhead 2000; Westneat and Stewart 2003). It follows that if a male can perceive that his pair female is unlikely to actively pursue EPCs and that she might even actively reject attempts by other males, then paternity could remain high despite little mate guarding effort. Such possibilities did not, however, appear to threaten the main pattern of better paternity prospects for males who express stronger paternity protection behaviours.

How does male quality relate to the presumed paternity protection behaviours?

Based on the widely invoked argument that females engage in EPCs for good-genes, females should prefer high quality males both as within-pair and extra-pair mates. We might therefore predict that, all else being equal, high quality males can afford to invest *less* in protecting their paternity, because their mate is less likely to solicit EPCs. This prediction assumes that EPCs are solicited by females, which generally seems to be the case (see Birkhead and Møller 1992; Hunter et al. 1993), although in some species EPCs appear to be forced (e.g. Alatalo et al. 1987; Morton 1987; Jones et al. 2012). If forced EPCs or harassment occur then females are expected to cooperate more willingly with male mate-guarding attempts. In such cases, we might predict that high quality males will protect their paternity *more* due to, for example, their greater energetic reserves. If so, paternity protection could be considered a signal of male quality to females. The second question answered in our meta-analysis sheds some light on the phenotypic relationship between investment in paternity protection and male quality. Higher quality males have a tendency to invest less in protecting their paternity. However, because the relationship between male quality and mate-guarding is negative while the relationship with copulation frequency is positive, we will look at each behaviour separately.

Copulation frequency

There are two potential explanations for the positive relationship between copulation frequency and all measures of male quality combined. First, frequent copulation might be of general benefit to males, with males of high quality having potentially larger energy stores and therefore able to copulate more frequently. Alternatively, in many species females solicit copulations, and they might solicit more copulations from high quality males to increase their share of paternity (assuming females sometimes mate with lower quality males for material benefits or to reduce harassment). It is interesting to note, however, that the relationship between copulation frequency and paternity is non-significant, potentially indicating that high quality males do not gain greater paternity from their more frequent copulations. We should also note though that the sample size for relationship between male quality and copulation frequency is small, so our statistical power remains low.

Mate guarding

Our results indicate that high quality males guard their mate *less*. Does this then mean that males of higher quality can afford to guard their mates less because these females are unlikely to look for EPCs? Our results cannot answer this question as it requires linking both male and female behavior during the fertile period to male quality. In the bluethroat (*Luscinia s. svecica*) older males, supposedly of higher quality, guard their mate less intensely but their females appear to cooperate by moving less, indicating that they do not actively search for EPCs (Johnsen et al. 2003). Higher quality males could thus reduce their mate-guarding intensity and invest in attempts to gain paternity with other females (Kempenaers et al. 1995; Wagner et al. 1996). Conversely, low quality males may guard their mate more intensely because they are unlikely to gain paternity elsewhere while their mates may be more likely to accept EPCs from other males (Kempenaers et al. 1995).

We looked at how five different categories of male quality correlated with mate-guarding intensity: age, colour, polygyny, size and song. Only polygyny and song had a significant negative relationship, while the relationships for age and colour were marginally non-significant, but still negative. The sample sizes for these five categories are relatively small, therefore we will only discuss those factors that have explicitly been linked to mate-guarding.

Polygyny in birds has been linked to a male's ability to guard as, according to the trade-off hypothesis (see Table 1), a male actively attracting a second female is unable to guard his primary mate with the same intensity as a monogamous male (Hasselquist and Sherman 2001; Birkhead and Møller 1992). Additionally, the female choice hypothesis suggests that females prefer to mate with high quality males (Hasselquist and Sherman 2001), so if polygynous males are more attractive their mates are unlikely to look for EPCs and will require less intense mate-guarding. Our analysis suggests that polygynous males guard less intense than socially monogamous males of the same species. We cannot distinguish between a pattern driven by males that are polygynous guarding less because they have little need for paternity protection, or guarding less because they are investing in attracting a second mate. Ideally we need empirical data on when a male attracts a second female. If this is outside of the primary female's fertile period than it is unlikely to influence male mate-guarding behaviour. Of the six studies linking polygyny to mate-guarding included in our meta-analysis only half mention whether the male starts to attract a second female during his primary mate's fertile period (Alatalo et al. 1987; Kempenaers et al. 1995; Pinxten and Eens 1997). In the remaining three studies the assumption is made that the male is guarding the primary female less because he is attracting a secondary female (Kempenaers et al. 1992; Dunn and Robertson 1993; Pilastro et al. 2002).

We found that intensively guarding males sing less. This finding supports the male announcement of fertility hypothesis (Møller 1991) whereby high quality males sing more and females mated to these males do not look for EPCs, and therefore require less mate-guarding. It is worth noting that song duets are sometimes considered a form of mate-guarding, although there is evidence that many well studied bird species use duetting to communicate with (potential) extra-pair mates (review: Dahlin and Benedict 2014).

Paternity protection and parental care

Males of many bird species provide care for eggs and/or offspring (Cockburn 2006). This behaviour is costly (Liker and Szekely 2005) so males are expected to provide care in relation to actual, or at least perceived, paternity (Whittingham et al. 1992; Westneat and Sherman 1993; Kempenaers and Sheldon 1997; Sheldon 2002; Griffin et al. 2013). Males are likely to use a range of cues to assess their likely paternity (Lifjeld et al. 1998; Sheldon 2002). Investment in presumed paternity protection behaviour is one such cue: a male guarding his mate intensely or copulating frequently should, all else being equal, be more certain of his paternity than one that has been separated from his mate for a period of time (Sheldon et al. 1997). Experimental studies suggest that certainty of paternity is, in fact, relatively easy to manipulate by temporary removing the male or his partner (e.g. Whittingham et al. 1993; Brylawski and Whittingham 2004; also see: Kempenaers and Sheldon 1997).

Our results suggest that males that (are able to) protect their paternity more intensely provide more care. This is most clear for studies where paternity protection was manipulated, for all types of paternity protection combined the relationship is marginally non-significant. The number of studies linking un-manipulated paternity protection to paternal care is, unfortunately, small (two studies for mate-guarding and five for copulation frequency). This is somewhat surprising given the considerable theoretical and empirical attention given to the relationship between paternity and paternal care (e.g. Houston 1995; Kempenaers and Sheldon 1996; 1997; Westneat and Sargent 1996; Lifjeld et al. 1998; Mauck et al. 1999; Kokko 1999; Sheldon 2002; Griffin et al. 2013; Matysioková and Remeš 2013), with the general conclusion that sufficiently good cues of paternity should make males respond to them in a phenotypically plastic way. Males that do not respond to cues of paternity may do so because they are unable to differentiate between extra-pair and their own offspring (Maynard-Smith 1977; Whittingham et al. 1992). Not caring might reduce offspring survival and a male’s reproductive success, especially in many species where biparental care seems obligate (Mauck et al. 1999; Arnold and Owens 2002). Ultimately, variation in paternity will only favour phenotypic plasticity in male care if males can redirect their investment to other fitness-enhancing activities (Kokko & Jennions 2008).

Publication bias and year effects

For some questions we found evidence for publication bias (see Results), however, while Egger's regression tests indicated a bias the trim-and-fill often did not identify any missing studies (standard random-effects meta-analyses). When trim-and-fill did identify missing studies the correction in all cases strengthened the observed trend, even leading to a significant mean effect. Our analyses also indicated some influence of year of publication in the standard random-effects meta-analyses. For our first question about paternity, more recent publications had more positive effect sizes. This may be explained by paternity analyses becoming cheaper and easier in the last decade, which is likely to increase the number of studies, their sample size and their accuracy. For the second question about male quality, technological advances may have played a role in creating larger effect sizes. For example, radio tracking collars have become smaller making it easier to track male and female movements accurately. For question three about parental care, earlier publications had more positive effect sizes, and the reasons for the trend are unclear.

The big picture: relating paternity, paternity protection, male quality, paternal care and other relevant factors.

There is a need to integrate existing knowledge on paternity, paternity protection, male quality, paternal care and other factors assumed to influence these traits. We have illustrated some of these relationships schematically in Figure 3.

Socially monogamous birds are presumed to avoid or reduce sperm competition by using putative paternity protection behaviours such as mate-guarding and frequent copulation. We show (bearing in mind that correlation is not causation) that these behaviours seem to be moderately effective at protecting a male's paternity. Due to costs associated with frequent copulation and mate-guarding (see above) the observed positive relationship would be expected.

Because of costs associated with putative paternity protection behaviours, we expect males to use them less intensely if they can afford to do so. Based on adaptive hypotheses for extra-pair copulations, females are expected to prefer to mate with high quality males (because quality is usually linked to genetic or material resources provided by the male), whether this is within the pair bond or outside of it. Does this then mean that higher quality males can invest less into paternity protection? Our results indeed suggest that high quality males use these putative paternity protection behaviours less. But does this then paradoxically imply that high quality males gain lower paternity? Models in which both male and female behaviours are allowed to evolve suggest that high quality males' effort in guarding can sometimes evolve to be lower than that of low quality males, yet realized paternity remains higher (because females paired to high quality males 'need less convincing' to remain faithful, Kokko & Morrell 2005). Apart from female behaviours remaining unknown in our data, several factors make definitive tests of such ideas hard. First, we are reporting on correlations (the exception being effects associated with experimental manipulation of mate guarding where causality can be inferred). Second, even if correlations are treated as indicative of causality, we would still need to test for the relationship between male quality and paternity directly. It is a general statistical rule, often overlooked, that knowing the pairwise correlations between two variables and a third focal variable (here 'paternity protection behaviour') does not allow us to determine the correlation between the two variables (explained by Langford et al. 2001).

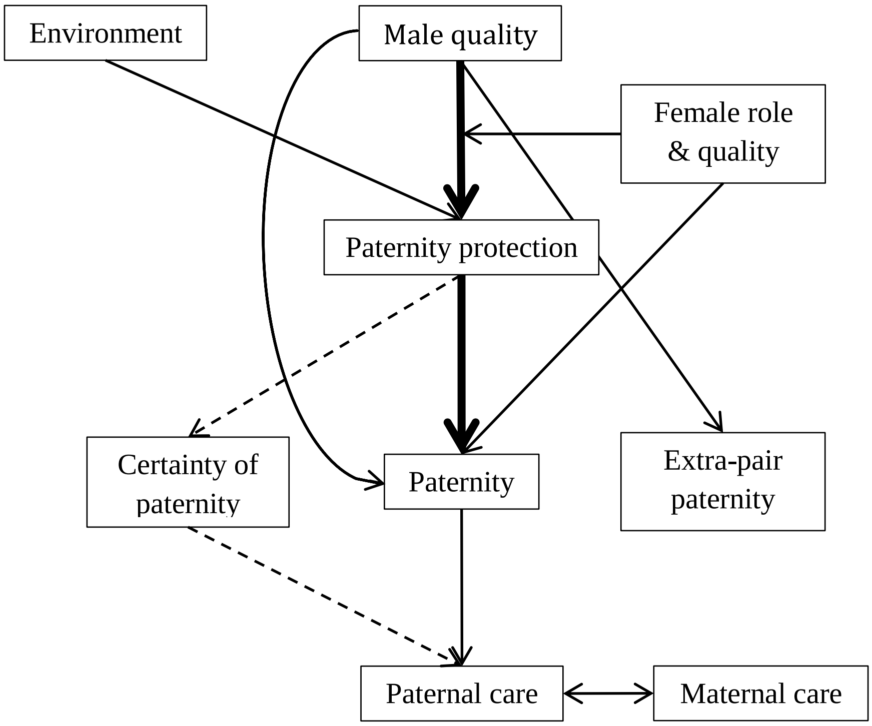

Figure 3. The inter-relationships between factors discussed in relation to paternity. The thick black lines represent two of the three relationships that we directly researched. Our third relationship is represented with the dashed line, this is because we have used paternity protection as a proxy for certainty of paternity. The thinner black lines represent relationships from existing theory, comparative and meta-analyses. The specifics of all these factors and inter-relationships are discussed in text.

There are at least three additional caveats as to why a negative relationship between paternity protection and male quality need not imply that males of high quality will have low paternity. First, the phenotypic relationship between paternity and mate-guarding can at best be classified as weak. Second, the manner in which paternity is measured could play a role: some studies only make a distinction between full and partial paternity (e.g. Møller and Tegelstrom 1997; Chuang-Dobbs et al. 2001). Thus high quality males could lose paternity but still, on average, have a higher proportion of within-pair paternity than lower quality males, but this is only apparent when results are based on the proportion of within-pair paternity. Third, high quality males may lose some paternity in their own nest but sire offspring elsewhere, resulting in higher offspring count for high quality males even if the paternity per nest remains meagre (Webster et al. 1995; Neff and Pitcher 2005; Balenger et al. 2009; Cleasby and Nakagawa 2012).

Male quality has been related to paternity in a number of studies. For example, Møller and Ninni (1998) included a range of measures of male quality, and found significant positive relationships for the factors male age, secondary sexual characters, wing length, and survival, while the relationship with polygyny was negative. However, Hasselquist and Sherman (2001) found that predominantly monogamous species had lower proportions of within-pair young than species with a larger proportion of polygyny. These two results regarding polygyny are not mutually exclusive: the patterns within species can be different from those among species. A recent meta-analysis reporting on the phenotypic correlation between male age and within-pair paternity did not find a significant relationship (Cleasby and Nakagawa 2012). Song has also been positively related to paternity (e.g. Hasselquist et al. 1996; Krokene et al. 1996; Gil et al. 2007; Hill et al. 2011), although a relatively recent meta-analysis and comparative analysis did not find this relationship (Garamszegi and Møller 2004). Akçay and Roughgarden (2007) compared extra-pair and within-pair male quality, they report a positive relationship between paternity and male age or size, however the relationship between paternity and body condition or sexual secondary characteristics was non-significant when correcting for publication bias. In general the support for a positive relationship between male quality and within-pair paternity seems quite weak.

The ‘good genes’ literature conventionally uses measures of male phenotypic condition and secondary sexual traits as male quality (Akçay and Roughgarden 2007). However whether these so called measures of quality are appropriate has been debated (Kokko and Lindström 1996; Brooks and Kemp 2001; Arnqvist and Rowe 2005). Additionally, some measures of quality may be more appropriate than others, for example we include a study where experimentally manipulated testosterone levels are related to mate-guarding intensity (Foerster and Kempenaers 2005). Although males with high levels of testosterone may be of higher quality, experimentally manipulating testosterone levels may not cause a male to be of high quality.

In Figure 3 we highlight that the female's role could be crucial to the observed relationship between paternity and male quality. This can be in the form of cooperation, i.e. the female makes no attempts at cuckolding her mate depending on his quality. However, a female pursuing extra-pair copulations is likely to succeed as males are unlikely to be guaranteed full paternity by intense mate-guarding or frequent copulation due to the costs of paternity protection behaviours (hence the direct line between female role and paternity in Figure 3). Why females accept or pursue EPCs is still vigorously debated (see Forstmeier et al. 2014 and references therein). Additionally, males may adjust the level of paternity protection in direct response to female quality, if the latter is linked to fecundity or otherwise related to reproductive success (Clutton-Brock 2009).

In this analysis we have not directly reported on the phenotypic correlation between paternity and paternal care (see Griffin et al. 2013 and Matysioková and Remeš2014 for meta-analyses of this relationship). Instead, we have used putative paternity protection behaviours as a 'proxy' for certainty of paternity (hence the dashed lines, Figure 3). Comparative studies and meta-analyses have demonstrated that males may reduce paternal care in response to extra-pair paternity, but that this is also dependent on other factors, such as the cost of paternal care and the likelihood of cuckoldry (Møller and Birkhead 1993b; Griffin et al. 2013; Matysioková and Remeš 2014). Paternal care has also been linked to male quality, as providing care to offspring is generally costly and males of good quality may be able to allocate more resources to care than lower quality males (Kempenaers and Sheldon 1997; Mauck et al. 1999; but see Kokko and Jennions 2008 for the counter argument that these males might gain more by investing disproportionately into seeking out additional matings). In some species females might be able to compensate for a reduction in male parental care and successfully fledge the brood (Ketterson and Nolan 1994), thereby reducing the costs to males of not providing care.

It is important to note that assessment of male quality is often context dependent. A female has to correctly assess the quality of her own mate as well as that of potential extra-pair mates (Slagsvold and Lifjeld 1997). Based on this fact certain environmental factors are commonly invoked to favour greater investment in paternity protection. For example, simply by providing many potential extra-pair mates nearby, both high local breeding density (Westneat and Sherman 1997; Møller and Ninni 1998; Griffith et al. 2002; Mougeot 2004; Neudorf 2004) and breeding synchrony (Stutchbury and Morton 1995; Stutchbury 1998; Møller and Ninni 1998; Neudorf 2004; but see Westneat and

Sherman 1997; Weatherhead and Yezerinac 1998) are expected to increase EPCs and thus extra-pair paternity . Similarly, nearest neighbour distance (e.g. Mougeot 2004) and the local adult sex ratio (ASR) or operational sex ratio (OSR) might also influence the value of paternity protection (Harts and Kokko 2013; Weir et al. 2011). In many bird species the ASR may not have a strong effect because unpaired or floater males are presumed to be non-preferred as extra-pair mates (Slagsvold and Lifjeld 1997; Kempenaers et al. 2001; Brekke et al. In press). But in species where extra-pair copulations are forced, male-biased ASR could favour greater paternity protection.

In conclusion, in socially monogamous birds presumed paternity protection behaviours do appear to protect a male's paternity, although perhaps weaker than expected ($r = 0.18$). These presumed paternity protection behaviours are negatively correlated with measures of male quality ($r = -0.19$), however splitting these paternity protection behaviours into mate-guarding and frequent copulation reveals different patterns. Mate-guarding remains negatively correlated with male quality ($r = -0.28$), while frequent copulation correlates positively with male quality ($r = 0.33$). The presumed paternity behaviours correlate positively with male parental care ($r = 0.23$), however this result is marginally non-significant. These patterns are consistent between the standard and multilevel (phylogenetic) random-effects meta-analyses. There are ample reviews, comparative and meta-analyses exploring the many hypotheses that attempt to explain within and extra-pair paternity in socially monogamous birds. Our results are an attempt to include the role of presumed paternity protection behaviours into the context of paternity, male quality, paternal care and other relevant factors.

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Supplement V – Data extracted from literature.

Effect sizes (*r*) for 87 papers covering all three questions. Note that the effect sizes have a direction, either positive, negative or unknown. For male quality the table includes on a few occasions 'color (1)' and 'color (2)' this is to identify that the data is based on different years and are treated as independent data points. 'No EPP' indicates there was no variation in the level of paternity within the study. References are below the table.

Species	ID & Ref.	study ID	Effect size (*r*)	N	Question	Paternity protection	Male quality	Publ. year	N1	N2	Orig. stat.
Acanthiza pusilla	1	1	-0.3398	17	2. Male quality	guard	age	2002	6	11	mean ± SD
Acanthiza pusilla	1	1	-0.0353	17	2. Male quality	guard	age	2002	6	11	mean ± SD
Acanthiza pusilla	1	1	-0.3522	17	2. Male quality	guard	age	2002	6	11	mean ± SD
Acanthiza pusilla	1	1	-0.0993	17	2. Male quality	guard	age	2002	6	11	mean ± SD
Acanthiza pusilla	1	1	?0.3413	17	2. Male quality	guard	size	2002	6	11	P
Acanthiza pusilla	1	1	?0.1408	17	2. Male quality	guard	size	2002	6	11	P
Acanthiza pusilla	1	1	?0.3733	17	2. Male quality	guard	size	2002	6	11	P
Acanthiza pusilla	1	1	?0.3341	17	2. Male quality	guard	size	2002	6	11	P
Acrocephalus arundinacues	2	2	-0.1237	130	1. Paternity	guard		1995	102	28	2 x 2
Acrocephalus schoenobaenus	3	3	?0.0932	15	1. Paternity	guard		2000	3	12	MWU
Acrocephalus schoenobaenus	3	3	?0.0186	15	1. Paternity	guard		2000	3	12	MWU
Acrocephalus sechellensis	4	4	0.7198	17	1. Paternity	manipulation		2007	8	9	Wald
Acrocephalus sechellensis	4	4	0.3099	17	1. Paternity	manipulation		2007	8	9	2 x 2
Acrocephalus sechellensis	5	5	-0.9055	7	2. Male quality	guard	size	2001			R^2
Agelaius phoeniceus	6	6	0.2708	15	1. Paternity	guard		1996			K τ
Agelaius phoeniceus	6	6	0.2377	15	1. Paternity	guard		1996			K τ
Agelaius phoeniceus	6	6	0.6217	15	1. Paternity	guard		1996			K τ
Agelaius phoeniceus	6	6	0.6340	15	1. Paternity	guard		1996			K τ
Agelaius phoeniceus	7	7	0.0865	24	1. Paternity	manipulation		1994	11	13	mean ± SD
Alca torda	8	8	-0.3200	21	3. Paternal care	copulation		1992			P r
Alca torda	8	8	0.0100	26	3. Paternal care	copulation		1992			P r
Alca torda	8	8	0.0600	24	3. Paternal care	copulation		1992			P r
Bubulcus ibis	9	9	0.5338	52	2. Male quality	copulation	color	2004			F
Bubulcus ibis	9	9	?0.0859	45	2. Male quality	guard	color	2004			F
Calidris mauri	10	10	0.7083	13	1. Paternity	guard		2002	2	11	mean ± SD
Ciconia ciconia	11	11	-0.1360	9	2. Male quality	copulation	size	1992			S r

Ciconia ciconia	11	11	0.4465	23	3. Paternal care	copulation		1992			S r
Columbia livia	12	12	-0.3222	12	3. Paternal care	copulation		1998			S r
Columbia livia	12	12	-0.2973	12	3. Paternal care	copulation		1998			S r
Cyanistes caeruleus	13	13	0.1232	34	2. Male quality	guard	hormone	2005	19	15	mean ± SD
Cyanistes caeruleus	13	13	-0.1147	34	2. Male quality	guard	hormone	2005	19	15	mean ± SD
Cyanistes caeruleus	13	13	-0.1232	34	2. Male quality	guard	hormone	2005	19	15	mean ± SD
Cyanistes caeruleus	14	1415	-0.6332	36	2. Male quality	guard	polygyny	1992	28	8	mean ± SD
Cyanistes caeruleus	14	1415	-0.1213	36	2. Male quality	guard	polygyny	1992	28	8	mean ± SD
Cyanistes caeruleus	14	1415	-0.7924	36	2. Male quality	guard	polygyny	1991	28	8	mean ± SD
Cyanistes caeruleus	15	1415	0.1986	26	1. Paternity	copulation		1995			S r
Cyanistes caeruleus	15	1415	0.2195	7	1. Paternity	copulation		1995			S r
Cyanistes caeruleus	15	1415	-0.0209	26	1. Paternity	guard		1995			S r
Cyanistes caeruleus	15	1415	0.0733	7	1. Paternity	guard		1995			S r
Cyanistes caeruleus	15	1415	-0.3645	26	1. Paternity	guard		1995			S r
Cyanistes caeruleus	15	1415	-0.3542	7	1. Paternity	guard		1995			S r
Cyanistes caeruleus	15	1415	0.5680	26	1. Paternity	guard		1995			S r
Cyanistes caeruleus	15	1415	-0.2403	7	1. Paternity	guard		1995			S r
Cyanistes caeruleus	15	1415	-0.5571	16	1. Paternity	manipulation		1995	8	8	mean ± SD
Cyanistes caeruleus	15	1415	-0.0105	36	2. Male quality	copulation	polygyny	1995	28	8	mean ± SD
Cyanistes caeruleus	15	1415	-0.2018	36	2. Male quality	guard	polygyny	1995	28	8	mean ± SD
Dendroica caerulescens	16	16.1	0.7397	8	1. Paternity	guard		2001	2	6	mean ± SD
Dendroica caerulescens	16	16.1	0.8947	8	1. Paternity	guard		2001	2	6	mean ± SD
Dendroica caerulescens	16	16.2	0.5774	16	1. Paternity	manipulation		2001	8	8	2 × 2
Dendroica caerulescens	16	16.2	0.3282	16	1. Paternity	manipulation		2001	8	8	mean ± SD
Dendroica caerulescens	17	17	-0.0625	8	2. Male quality	guard	size	2001	4	4	MWU
Dendroica caerulescens	17	17	?0.5625	8	2. Male quality	guard	size	2001	4	4	MWU
Emberiza citrinella	18	18	-0.2568	50	2. Male quality	guard	age	1992	17	33	mean ± SD
Emberiza citrinella	18	18	-0.1498	50	2. Male quality	guard	age	1992	17	33	mean ± SD
Emberiza schoeniclus	19	19	-0.9701	18	2. Male quality	guard	age	2006	8	10	mean ± SD
Emberiza schoeniclus	20	20	0.4960	21	1. Paternity	guard		2005			t
Empidonax virescens	21	21	0.0000	7	1. Paternity	guard		2009	1	6	mean ± SD
Ficedula albicollis	22	22	0.3256	42	3. Paternal care	manipulation		1997	17	25	F
Ficedula albicollis	22	22	0.3475	42	3. Paternal care	manipulation		1997	17	25	F
Ficedula hypoleuca	23	23	-0.2042	26	2. Male quality	guard	polygyny	1987	5	21	mean ± SD
Ficedula hypoleuca	24	24	0.4938	54	1. Paternity	manipulation		1997	27	27	2 x 2
Ficedula hypoleuca	25	25	0.1398	23	3. Paternal care	manipulation		1998	17	6	mean ± SD

Ficedula hypoleuca	25	25	0.1703	23	3. Paternal care	manipulation		1998	17	6	mean ± SD
Ficedula hypoleuca	26	26	0.1037	39	1. Paternity	manipulation		2001	19	20	2 x 2
Fringella coelebs	27	27	-0.3961	6	2. Male quality	guard	age	1992	1	5	mean ± SD
Fringella coelebs	27	27	-0.2106	6	2. Male quality	guard	age	1992	1	5	mean ± SD
Fulmarus glacialis	28	28	0.0000	19	1. Paternity	copulation		1992			NO EPP
Gavia immer	29	29	0.0000	36	1. Paternity	copulation		1997			NO EPP
Gavia immer	29	29	0.0000	36	1. Paternity	guard		1997			NO EPP
Geothlypis trichas	30	30	0.2000	10	1. Paternity	guard		2006	5	5	2 x 2
Geothlypis trichas	30	30	-0.2000	10	1. Paternity	guard		2006	5	5	2 x 2
Geothlypis trichas	30	30	-0.2363	5	1. Paternity	guard		2006	2	3	mean ± SD
Geothlypis trichas	30	30	0.9144	5	1. Paternity	guard		2006	3	2	mean ± SD
Geothlypis trichas	30	30	0.4898	10	1. Paternity	guard		2006	5	5	mean ± SD
Geothlypis trichas	30	30	-0.0917	10	1. Paternity	guard		2006	5	5	mean ± SD
Geothlypis trichas	30	30	?0.3352	13	2. Male quality	guard	color	2006	8	5	t
Geothlypis trichas	30	30	?0.0121	13	2. Male quality	guard	size	2006	8	5	t
Geothlypis trichas	30	30	?0.0024	13	2. Male quality	guard	size	2006	8	5	t
Geothlypis trichas	30	30	0.2406	15	2. Male quality	guard	size	2006	7	8	mean ± SD
Geothlypis trichas	30	30	-0.5114	13	2. Male quality	guard	size	2006	8	5	mean ± SD
Hirundo rustica	31	31	-0.0900	51	2. Male quality	guard	age	1987			r
Hirundo rustica	31	31	0.0900	51	2. Male quality	guard	size	1987			r
Hirundo rustica	31	31	0.0900	51	2. Male quality	guard	size	1987			r
Hirundo rustica	31	31	-0.0200	51	2. Male quality	guard	size	1987			r
Hirundo rustica	31	31	0.0900	51	2. Male quality	guard	size	1987			r
Hirundo rustica	32	32.1	0.4400	38	3. Paternal care	copulation		1988			r
Hirundo rustica	32	32.1	0.6000	38	3. Paternal care	copulation		1988			r
Hirundo rustica	32	32.2	0.8645	20	3. Paternal care	manipulation		1988	10	10	mean ± SD
Hirundo rustica	32	32.2	0.7164	20	3. Paternal care	manipulation		1988	10	10	mean ± SD
Hirundo rustica	33	33	-0.0921	38	1. Paternity	copulation		1997	17	21	mean ± SD
Hirundo rustica	33	33	-0.1898	38	1. Paternity	guard		1997	17	21	mean ± SD
Hirundo rustica	34	34	0.5200	26	2. Male quality	guard	hormone	1995			r
Hirundo rustica	34	34	-0.1200	26	2. Male quality	guard	size	1995			r
Jacana jacana	35	35	0.0000	14	1. Paternity	copulation		1998			NO EPP
Luscinia svecica	36	36	-0.3333	13	2. Male quality	guard	color	1995	7	6	MWU
Luscinia svecica	37	37.1	-0.0278	12	2. Male quality	guard	color (1)	1997	6	6	MWU
Luscinia svecica	37	37.1	-0.1667	12	2. Male quality	guard	color (1)	1997	6	6	MWU
Luscinia svecica	37	37.1	-0.5417	10	2. Male quality	guard	color (1)	1997	6	4	MWU

Luscinia svecica	37	37.2	-0.2500	15	2. Male quality	guard	color (2)	1997	8	7	MWU
Luscinia svecica	37	37.2	-0.2321	15	2. Male quality	guard	color (2)	1997	8	7	MWU
Luscinia svecica	37	37.2	-0.2041	14	2. Male quality	guard	color (2)	1997	7	7	MWU
Luscinia svecica	37	37.3	-0.6775	27	2. Male quality	guard	song	1997			S r
Luscinia svecica	38	38.1	0.5680	12	1. Paternity	guard		1998			S r
Luscinia svecica	38	38.1	0.4872	12	1. Paternity	guard		1998			S r
Luscinia svecica	38	38.1	0.3850	12	1. Paternity	guard		1998			S r
Luscinia svecica	38	38.1	-0.3772	13	2. Male quality	guard	color (1)	1998	7	6	mean ± SD
Luscinia svecica	38	38.1	-0.6088	13	2. Male quality	guard	color (1)	1998	7	6	mean ± SD
Luscinia svecica	38	38.1	-0.4888	13	2. Male quality	guard	color (1)	1998	7	6	mean ± SD
Luscinia svecica	38	38.2	-0.1630	17	2. Male quality	guard	color (2)	1998	6	11	mean ± SD
Luscinia svecica	38	38.2	-0.3832	17	2. Male quality	guard	color (2)	1998	6	11	mean ± SD
Luscinia svecica	38	38.2	-0.2182	16	2. Male quality	guard	color (2)	1998	6	10	mean ± SD
Luscinia svecica	39	39	?0.0408	27	1. Paternity	guard		2003			P
Luscinia svecica	39	39	?0.0943	27	1. Paternity	guard		2003			P
Luscinia svecica	39	39	-0.6285	32	2. Male quality	guard	age	2003	10	22	mean ± SD
Luscinia svecica	39	39	0.0419	11	2. Male quality	guard	color	2003			S r
Luscinia svecica	39	39	-0.2195	11	2. Male quality	guard	color	2003			S r
Luscinia svecica	39	39	0.0524	11	2. Male quality	guard	color	2003			S r
Luscinia svecica	39	39	-0.6280	16	2. Male quality	guard	size	2003			S r
Luscinia svecica	39	39	-0.2299	28	2. Male quality	guard	size	2003			S r
Luscinia svecica	39	39	0.2091	28	2. Male quality	guard	size	2003			S r
Luscinia svecica	39	39	-0.5075	28	2. Male quality	guard	size	2003			S r
Luscinia svecica	40	40	0.2127	48	1. Paternity	manipulation		2008	23	25	2 x 2
Luscinia svecica	40	40	0.2958	48	1. Paternity	manipulation		2008	23	25	F
Oenanthe oenanthe	41	41	0.3200	12	1. Paternity	guard		1998	3	9	mean ± SD
Oenanthe oenanthe	41	41	?0.2849	12	2. Male quality	guard	age	1998			t
Oenanthe oenanthe	41	41	0.0300	12	2. Male quality	guard	size	1998			r
Oenanthe oenanthe	42	42	0.3016	26	1. Paternity	manipulation		1999	16	10	2 x 2
Parus cristatus	43	43	0.7500	17	2. Male quality	copulation	size	1997			r
Parus montanus	44	44	-0.2910	47	2. Male quality	guard	age	1995	22	25	F
Parus montanus	44	44	-0.2509	47	2. Male quality	guard	age	1995	22	25	F
Passer domesticus	45	45	0.5100	43	2. Male quality	copulation	size	2011			r
Passer domesticus	45	45	0.4800	43	2. Male quality	guard	size	2011			r
Passer domesticus	46	46	0.7069	12	1. Paternity	copulation		2002			S r
Passer domesticus	46	46	0.6280	12	1. Paternity	guard		2002			S r

Passer domesticus	46	46	0.1047	14	2. Male quality	copulation	size	2002			S r
Passer domesticus	46	46	0.7069	14	2. Male quality	guard	size	2002			S r
Passerina cyanea	47	47	-0.0653	67	2. Male quality	guard	age	1988	18	49	mean ± SD
Petronia petronia	48	48	0.0202	39	2. Male quality	copulation	polygyny	2002	9	30	mean ± SD
Petronia petronia	48	48	-0.4196	37	2. Male quality	guard	polygyny	2002	9	28	mean ± SD
Phylloscopus trochilus	49	49	-0.0580	20	1. Paternity	manipulation		1997	5	15	2 x 2
Phylloscopus trochilus	50	50	-0.4913	20	2. Male quality	guard	song	1999			S r
Plectrophenax nivalis	51	51	-0.6950	63	2. Male quality	guard	song	2009			P r
Plectrophenax nivalis	51	51	-0.1841	63	3. Paternal care	guard		2009			F
Progne subis	52	52	-0.2420	22	2. Male quality	guard	age	1987	9	13	mean ± SD
Progne subis	52	52	-0.5400	8	3. Paternal care	guard		1987	4	4	r
Progne subis	53	53	0.2629	13	1. Paternity	guard		1990			r
Progne subis	53	53	0.2748	13	2. Male quality	guard	age	1990	7	6	mean ± SD
Progne subis	54	54	0.6775	11	1. Paternity	guard		1996			S r
Progne subis	54	54	-0.3743	58	2. Male quality	guard	age	1996	25	33	mean ± SD
Prunella modularis	55	55	0.0000	15	1. Paternity	guard		1989			NO EPP
Prunella modularis	56	56	0.9999	9	3. Paternal care	manipulation		1992	2	7	2 x 2
Prunella modularis	56	56	0.0000	13	3. Paternal care	manipulation		1992	6	7	2 x 2
Remiz pendulinus	57	57	0.0052	34	1. Paternity	copulation		1997			S r
Remiz pendulinus	57	57	-0.0628	34	1. Paternity	guard		1997			S r
Sericornis frontalis	58	58	-0.5075	6	1. Paternity	guard		1998			S r
Serinus serinus	59	59	0.0000	16	1. Paternity	copulation		2003			NO EPP
Serinus serinus	59	59	0.0000	16	1. Paternity	guard		2003			NO EPP
Serinus serinus	59	59	0.0000	16	1. Paternity	guard		2003			NO EPP
Setophaga ruticilla	60	60	0.0456	13	1. Paternity	guard		2010	5	8	mean ± SD
Setophaga ruticilla	60	60	-0.0442	13	1. Paternity	guard		2010	5	8	mean ± SD
Sialia mexicana	61	61	0.0325	19	3. Paternal care	manipulation		2003	6	13	mean ± SD
Sialia mexicana	61	61	0.1785	60	3. Paternal care	manipulation		2003	32	28	mean ± SD
Sialia sialis	62	62	-0.1116	15	3. Paternal care	manipulation		1998	7	8	F
Sialia sialis	62	62	0.0250	15	3. Paternal care	manipulation		1998	7	8	t
Sialia sialis	63	63	0.4284	25	1. Paternity	manipulation		1996	11	14	2 x 2
Sialia sialis	64	64	0.3822	31	3. Paternal care	manipulation		1998	13	18	mean ± SD
Sialia sialis	64	64	0.0694	31	3. Paternal care	manipulation		1998	13	18	mean ± SD
Sialia sialis	65	65	-0.2382	8	1. Paternity	guard		1994			S r
Speheniscus humboldti	66	66	0.0000	21	1. Paternity	copulation		1999			NO EPP
Sterna hirundo	67	67	0.6379	18	2. Male quality	copulation	age	2002			S r

Sturnus vulgaris	68	68	-0.1527	8	3. Paternal care	copulation		1995			S r
Sturnus vulgaris	69	69	0.2585	6	1. Paternity	copulation		1993	1	5	mean ± SD
Sturnus vulgaris	70	70	0.6755	14	2. Male quality	copulation	polygyny	1997	5	9	mean ± SD
Sturnus vulgaris	70	70	-0.7926	15	2. Male quality	guard	polygyny	1997	7	8	mean ± SD
Sturnus vulgaris	70	70	-0.3201	14	2. Male quality	guard	polygyny	1997	7	7	mean ± SD
Sturnus vulgaris	70	70	-0.1243	14	2. Male quality	guard	polygyny	1997	7	7	mean ± SD
Sula nebouxii	71	71	0.0953	13	3. Paternal care	manipulation		2001	5	8	mean ± SD
Sula nebouxii	71	71	0.5348	33	3. Paternal care	manipulation		2001	16	17	2 x 2
Tachycineta bicolor	72	72	0.4161	34	1. Paternity	copulation		2009			F
Tachycineta bicolor	73	73	-0.1369	35	2. Male quality	copulation	polygyny	1993	7	28	mean ± SD
Tachycineta bicolor	73	73	-0.5748	22	2. Male quality	guard	polygyny	1993	7	15	mean ± SD
Tachycineta bicolor	73	73	-0.3559	25	2. Male quality	guard	polygyny	1993	7	18	mean ± SD
Tachycineta bicolor	74	74	-0.1256	21	1. Paternity	copulation		1994			S r
Tachycineta bicolor	74	74	0.0838	21	1. Paternity	guard		1994			S r
Tachycineta bicolor	75	75	-0.1598	44	3. Paternal care	manipulation		1998	23	21	F
Tachycineta bicolor	75	75	-0.2414	46	3. Paternal care	manipulation		1998	25	21	t
Tachycineta bicolor	76	76	0.0000	26	1. Paternity	manipulation		1992	10	16	2 x 2
Tachycineta bicolor	77	77	-0.0314	12	1. Paternity	copulation		1993			S r
Tachycineta bicolor	78	78	0.1200	15	3. Paternal care	manipulation		1993			r
Tachycineta bicolor	78	78	-0.0520	11	3. Paternal care	manipulation		1993	6	5	mean ± SD
Tachycineta bicolor	78	78	0.0788	8	3. Paternal care	manipulation		1993	4	4	mean ± SD
Tachycineta bicolor	78	78	-0.2592	10	3. Paternal care	manipulation		1993	5	5	mean ± SD
Tachycineta bicolor	78	78	0.0000	7	3. Paternal care	manipulation		1993	3	4	mean ± SD
Troglodytes aedon	79	79	0.3651	24	1. Paternity	manipulation		2004	15	9	2 x 2
Troglodytes aedon	79	79	-0.1917	11	3. Paternal care	manipulation		2004	6	5	mean ± SD
Troglodytes aedon	79	79	0.2509	12	3. Paternal care	manipulation		2004	7	5	mean ± SD
Troglodytes aedon	79	79	-0.0837	11	3. Paternal care	manipulation		2004	6	5	mean ± SD
Troglodytes aedon	79	79	0.2892	12	3. Paternal care	manipulation		2004	7	5	mean ± SD
Turdus merula	80	80	-0.2037	21	2. Male quality	guard	age	2001	3	18	MWU
Turdus merula	80	80	-0.3148	21	2. Male quality	guard	age	2001	3	18	MWU
Vanellus vanellus	81	81	0.2614	19	2. Male quality	copulation	polygyny	2001	7	12	mean ± SD
Vanellus vanellus	81	81	0.3327	19	2. Male quality	copulation	polygyny	2001	7	12	mean ± SD
Wilsonia citrina	82	82	0.1491	14	1. Paternity	guard		2008			2 x 2
Wilsonia citrina	82	82	0.5449	14	1. Paternity	guard		2008			S r
Wilsonia citrina	82	82	-0.2559	17	2. Male quality	guard	song	2008			S r
Wilsonia citrina	82	82	0.5861	17	2. Male quality	guard	song	2008			S r

Wilsonia citrina	83	83	?0.7000	11	2. Male quality	guard	age	2002	5	6	MWU
Wilsonia citrina	83	83	?0.5333	11	2. Male quality	guard	age	2002	5	6	MWU
Wilsonia citrina	83	83	?0.5333	11	2. Male quality	guard	age	2002	5	6	MWU
Wilsonia citrina	84	84	-0.2776	9	1. Paternity	guard		1997	2	7	mean ± SD
Wilsonia citrina	84	84	0.5774	12	2. Male quality	guard	age	1997	6	6	2 x 2
Wilsonia citrina	84	84	-0.0419	13	2. Male quality	guard	size	1997			S r
Wilsonia citrina	84	84	-0.0962	13	2. Male quality	guard	size	1997	10	3	mean ± SD
Wilsonia citrina	84	84	0.3953	13	2. Male quality	guard	size	1997			S r
Wilsonia citrina	84	84	0.2751	13	2. Male quality	guard	size	1997	10	3	mean ± SD
Wilsonia citrina	84	84	-0.2922	13	2. Male quality	guard	size	1997			S r
Wilsonia citrina	84	84	0.4683	13	2. Male quality	guard	size	1997	10	3	mean ± SD
Wilsonia citrina	85	85	-0.3649	13	1. Paternity	guard		2005	6	7	t
Wilsonia citrina	85	85	?0.4911	13	1. Paternity	guard		2005	6	7	t
Wilsonia citrina	86	86	-0.0838	9	2. Male quality	guard	age	1998			S r
Wilsonia citrina	86	86	-0.1256	9	2. Male quality	guard	age	1998			S r
Wilsonia citrina	86	86	0.4261	9	2. Male quality	guard	size	1998			S r
Wilsonia citrina	86	86	-0.4261	9	2. Male quality	guard	size	1998			S r
Wilsonia citrina	86	86	0.1882	10	2. Male quality	guard	song	1998			S r
Wilsonia citrina	86	86	-0.1047	10	2. Male quality	guard	song	1998			S r
Zosterops lateralis	87	87	0.0000	11	1. Paternity	copulation		2001			NO EPP
Zosterops lateralis	87	87	0.0000	9	1. Paternity	guard		2001			NO EPP
Zosterops lateralis	87	87	0.0000	9	1. Paternity	guard		2001			NO EPP

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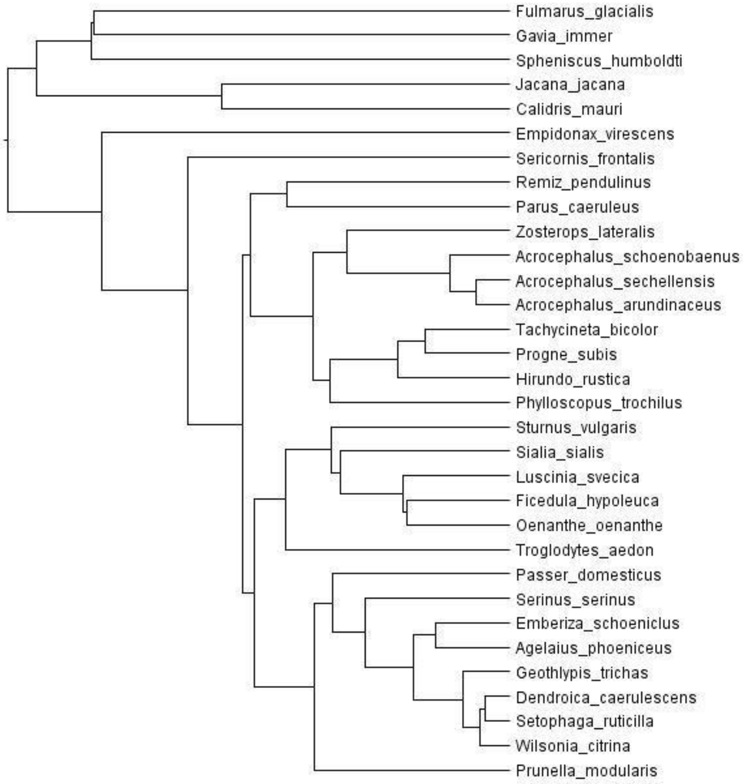
Supplement VI – Supplementary figures and results

Figure S1. The Ericsson backbone phylogenetic trees used for each of the three questions.

Q1.



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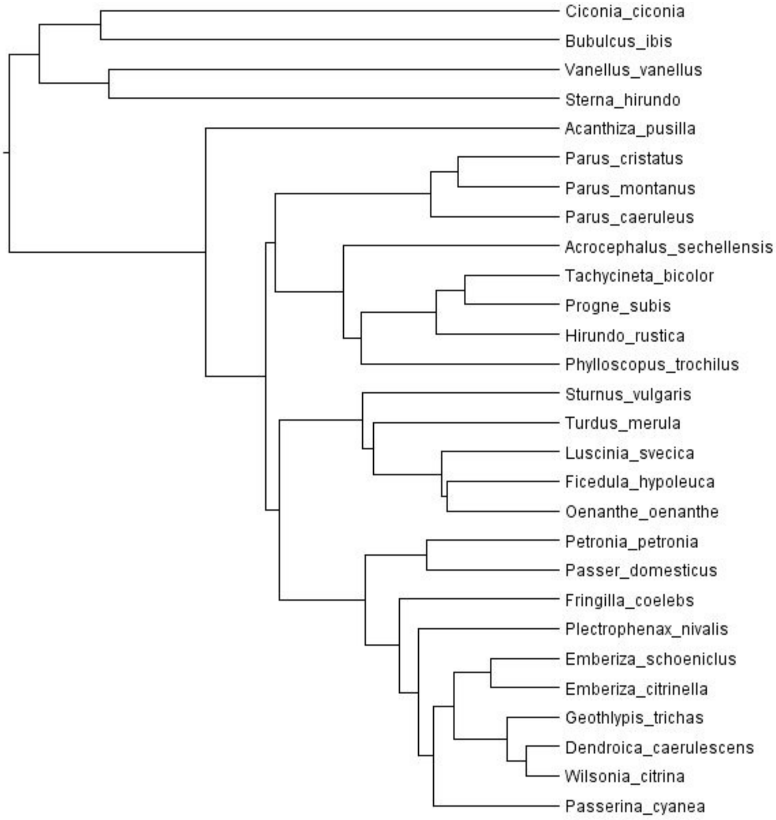

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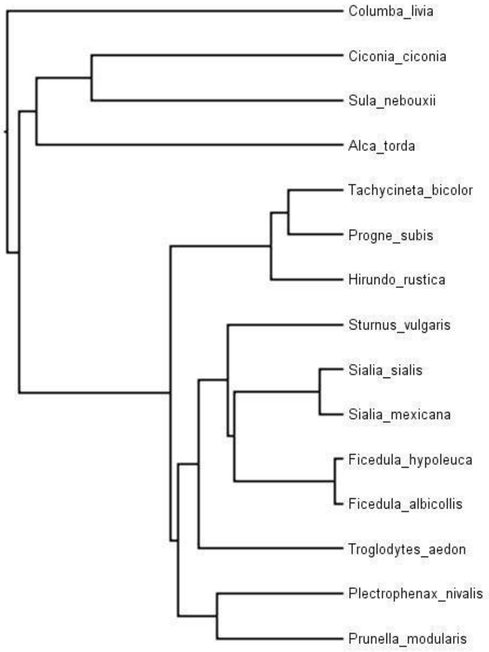
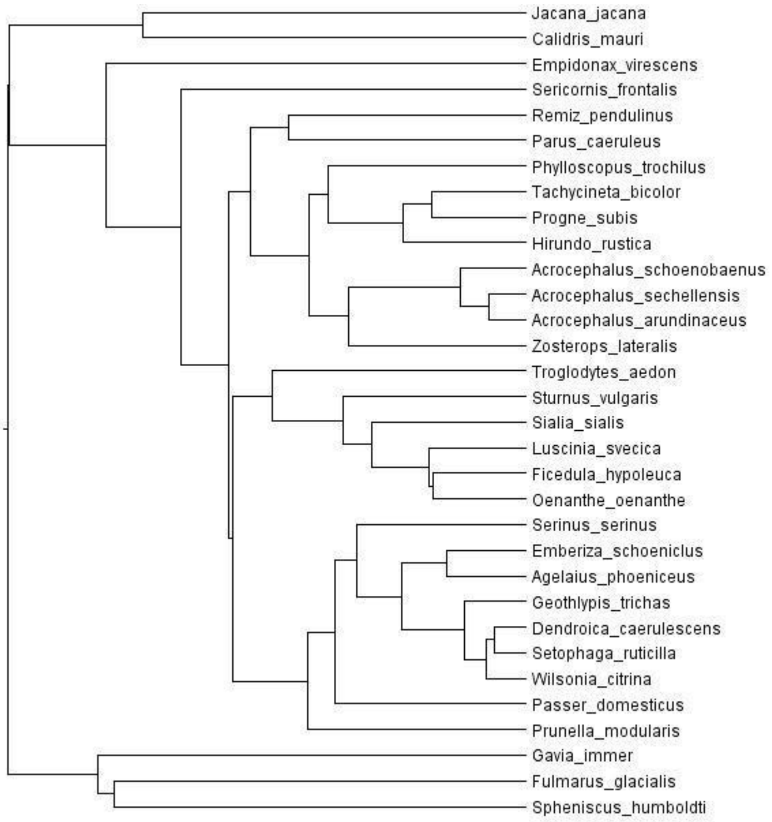


Figure S2. The Hackett backbone phylogenetic trees used for each of the three questions.

Q1.



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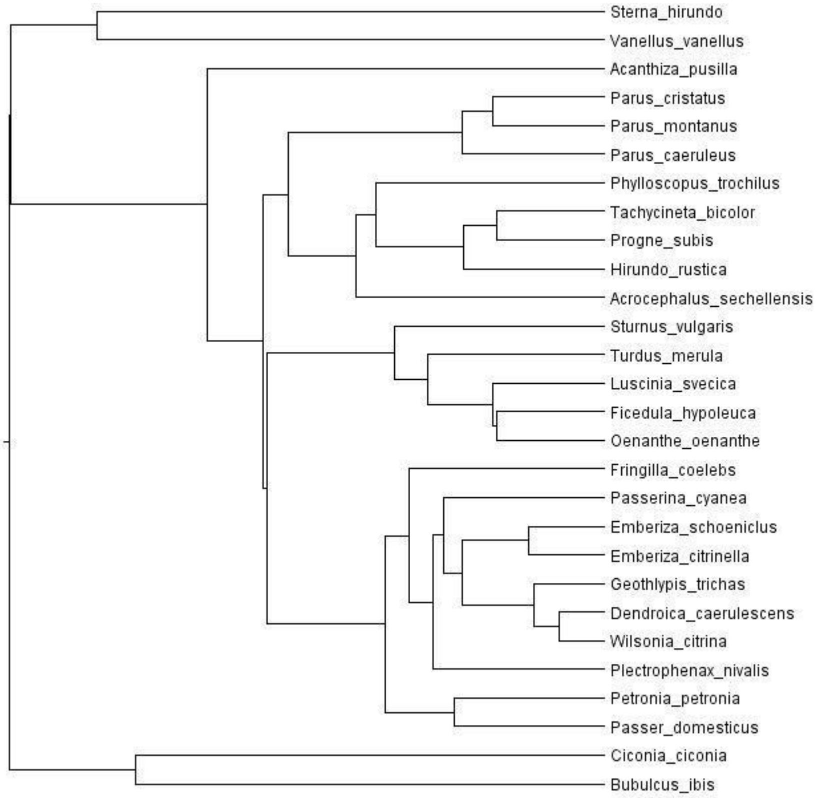

Sterna_hirundo
Vanellus_vanellus
Acanthiza_pusilla
Parus_cristatus
Parus_montanus
Parus_caeruleus
Phylloscopus_trochilus
Tachycineta_bicolor
Progne_subis
Hirundo_rustica
Acrocephalus_sechellensis
Sturnus_vulgaris
Turdus_merula
Luscinia_svecica
Ficedula_hypoleuca
Oenanthe_oenanthe
Fringilla_coelebs
Passerina_cyanea
Emberiza_schoeniclus
Emberiza_citrinella
Geothlypis_trichas
Dendroica_caerulescens
Wilsonia_citrina
Plectrophenax_nivalis
Petronia_petronia
Passer_domesticus
Ciconia_ciconia
Bubulcus_ibis

Q3.

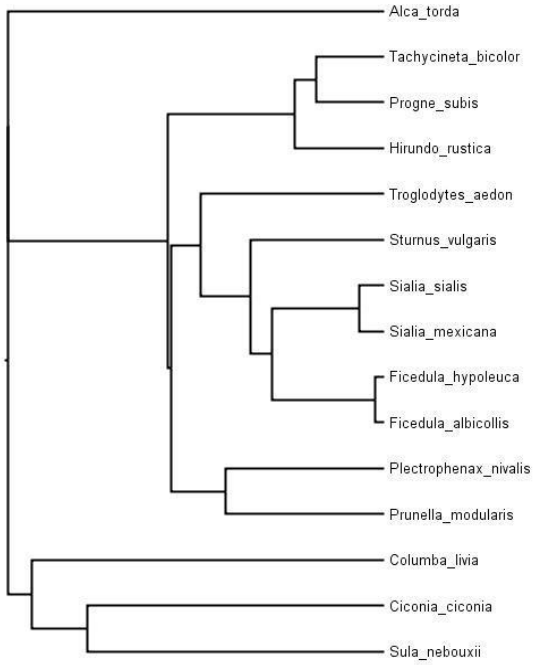
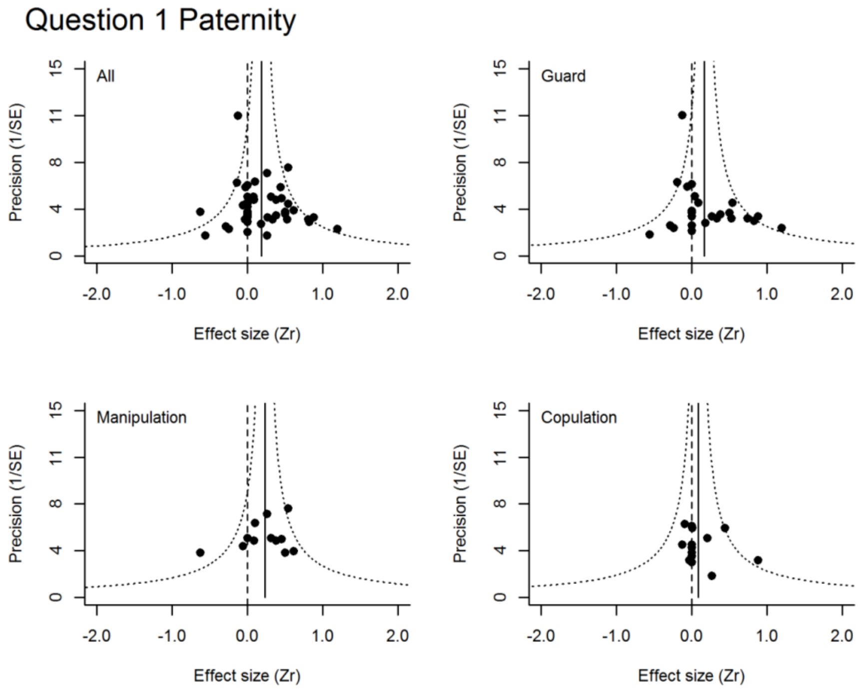
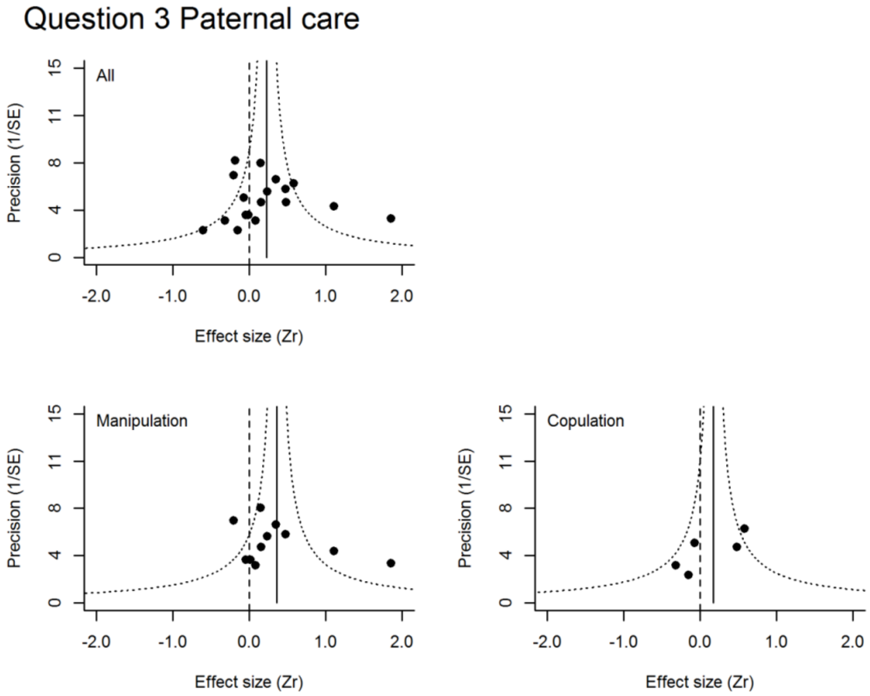

Alca_torda
Tachycineta_bicolor
Progne_subis
Hirundo_rustica
Troglodytes_aedon
Sturnus_vulgaris
Sialia_sialis
Sialia_mexicana
Ficedula_hypoleuca
Ficedula_albicollis
Plectrophenax_nivalis
Prunella_modularis
Columba_livia
Ciconia_ciconia
Sula_nebouxii

Figure S3. Funnel plots for each of the three questions in the random-effects meta-analyses, Question 2 is separate on the next page. "All " refers to the meta-analysis with all categories combined and other labels refer to the categories that we ran separate meta-analyses for. Note the effect size is given as Zr.


Question 1 Paternity


Question 3 Paternal care

Question 2 Male quality

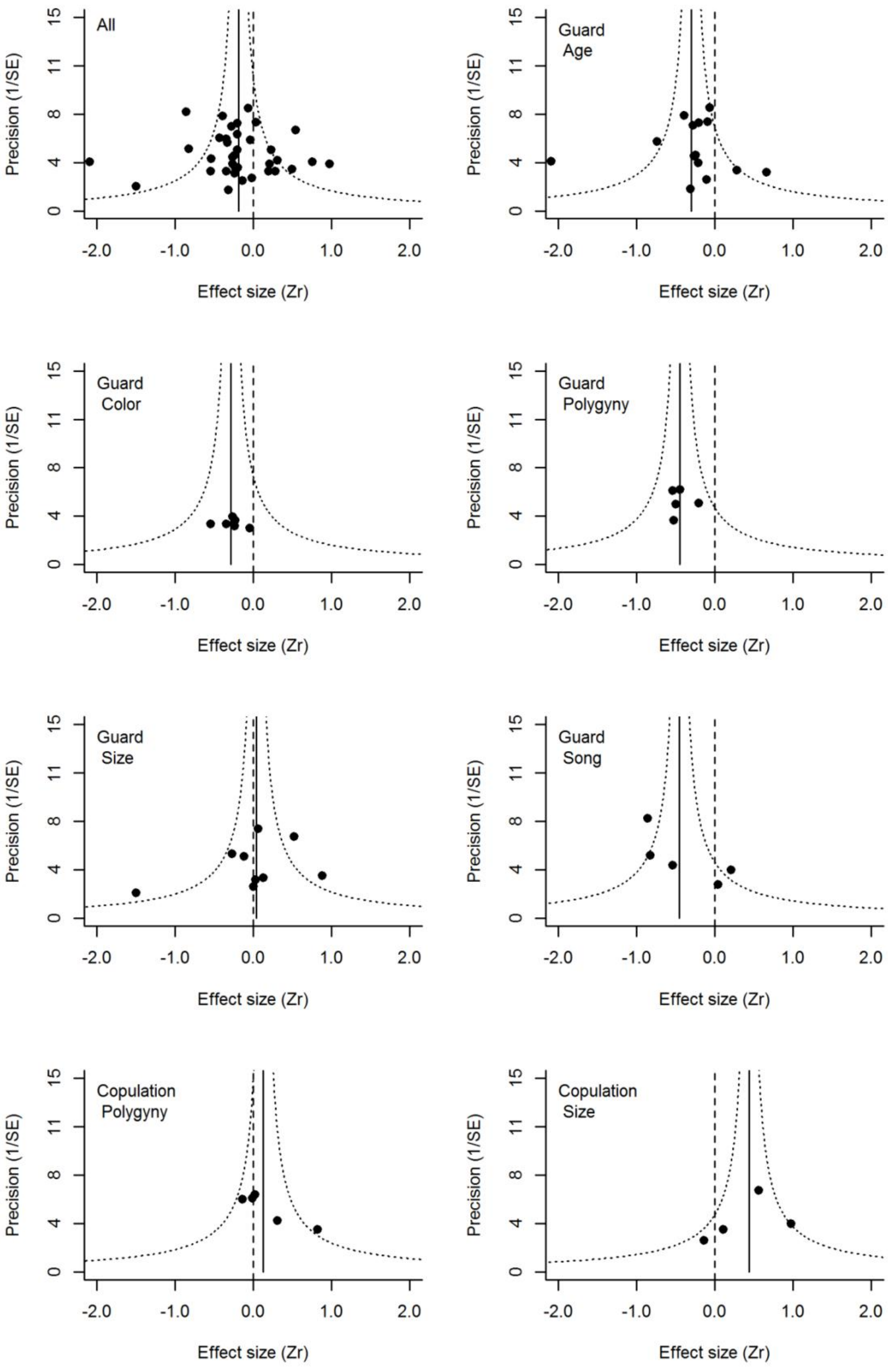


Figure S4 Funnel plots for each of the three questions in the multi-level meta-analyses, plots use the meta-analytic residuals of Model 1 and Model 3 (phylogenetic, Ericsson tree). Note the effect size is given as Zr.

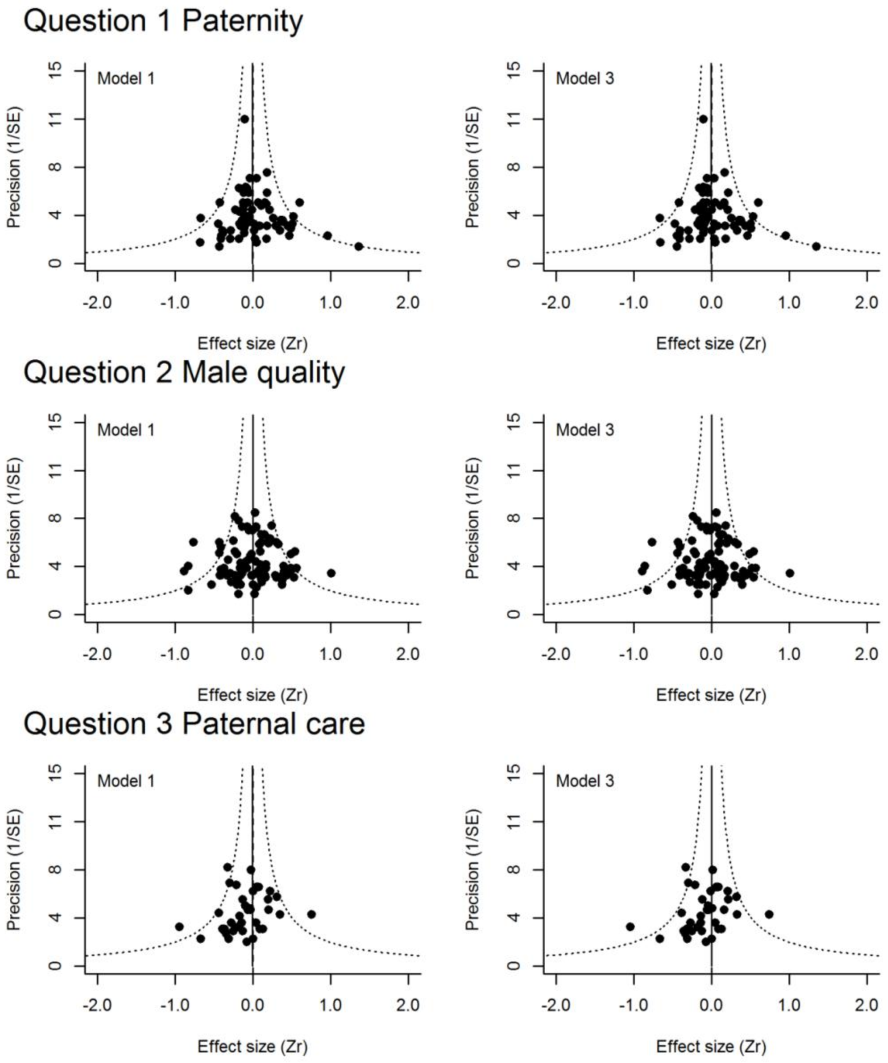


Table S1. Results from the multilevel meta-analyses for each of the questions taking into account that effect sizes from a single study may be correlated, paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care, for Models 1 and 3 (null model and phylogenetic null model (E and H refer to the Ericsson and Hackett phylogeny), respectively). Q = question, M = model, *k* = the number of effect sizes, *m* = the number of species and *n* = the number of broods. L. CI and U. CI are the lower and upper confidence intervals respectively.

Q	M	Data set	*k*	*m*	*n*	Mean (*r*)	L. CI	U. CI	I^2_{study} (%)	I^2_{species} (%)	I^2_{ES} (%)	I^2_{phylo} (%)	I^2_{total} (%)	H^2 (%)
1	1	1	76	31	1144	0.186	0.088	0.280	9.70	9.52	22.14		41.35	
		2	81	32	1199	0.176	0.078	0.271	9.75	8.50	20.46		38.71	
		3	81	32	1199	0.167	0.071	0.281	10.74	9.14	19.08		38.96	
	3	1E	76	31	1144	0.176	0.012	0.330	8.78	8.38	20.90	8.99	47.05	18.44
		2E	81	32	1199	0.165	0.018	0.317	8.52	7.88	19.13	8.32	43.84	18.67
		3E	81	32	1199	0.164	-0.008	0.312	24.86	10.39	8.40	8.03	51.67	20.08
		1H	76	31	1144	0.168	-0.003	0.302	8.15	8.21	20.76	8.92	46.03	18.34
2	1	1	96	28	2262	-0.162	-0.340	0.011	4.03	46.90	34.98		85.90	
	3	1E	96	28	2262	-0.046	-0.383	0.380	3.16	33.05	31.46	19.64	87.32	37.87
		1H	96	28	2262	-0.059	-0.372	0.427	3.27	32.78	31.72	19.37	87.14	37.57
3	1	1	38	15	869	0.210	-0.062	0.455	15.73	18.84	12.23		46.80	
	3	1E	38	15	869	0.196	-0.204	0.493	14.35	16.63	10.11	17.83	58.92	28.02
		1H	38	15	869	0.206	-0.141	0.517	13.79	15.78	10.45	18.68	58.70	26.80

Table S2. Results from the phylogenetic multilevel meta-analyses for each of the questions taking into account that effect sizes from a single study may be correlated, paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care, for Models 2 and 4 (multi-level meta-regression and phylogenetic multi-level meta-regression (E and H refer to the Ericsson and Hackett phylogeny), respectively). Q = question, M = model, k = the number of effect sizes, m = the number of species and n = the number of broods. L. CI and U. CI are the lower and upper confidence intervals respectively.

Q	M	Data set	*k*	Paternity protection	Mean (*r*)	L CI	U CI	I^2_{study}	I^2_{species}	$I^2_{\text{Effect size}}$	I^2_{phylo}	I^2_{total}	H^2
1	2	1	46	Guard	0.193	0.061	0.317						
			15	Manipulation	0.204	0.016	0.363						
			15	Copulation	0.187	0.012	0.337						
				Year	0.087	-0.010	0.019	8.68	9.06	21.93		39.66	
		2	51	Guard	0.168	0.041	0.289						
			15	Manipulation	0.206	0.026	0.343						
			15	Copulation	0.173	-0.013	0.316						
				Year	0.084	-0.018	0.174	8.72	7.97	20.20		36.90	
		3	51	Guard	0.149	0.021	0.274						
			15	Manipulation	0.207	0.053	0.364						
			15	Copulation	0.171	0.011	0.339						
				Year	0.078	-0.015	0.178	9.28	9.05	18.56		36.89	

Q	M	Data set	k	Paternity protection	Mean (r)	L CI	U CI	I^2_{study}	I^2_{species}	$I^2_{\text{Effect size}}$	I^2_{phylo}	I^2_{total}	H^2
1	4	1E	46	Guard	0.180	0.009	0.343						
			15	Manipulation	0.179	-0.075	0.371						
			15	Copulation	0.176	-0.022	0.376						
				Year	0.085	-0.006	0.180	8.69	9.36	22.57	8.54	40.62	18.82
		2E	51	Guard	0.161	-0.015	0.328						
			15	Manipulation	0.193	-0.028	0.392						
			15	Copulation	0.173	-0.020	0.359						
				Year	0.080	-0.011	0.173	8.05	8.86	20.40	7.70	37.30	19.64
	4	1H	46	Guard	0.184	0.021	0.355						
			15	Manipulation	0.193	-0.044	0.392						
			15	Copulation	0.184	-0.015	0.372						
				Year	0.084	-0.026	0.180	9.03	9.21	22.30	8.12	40.53	18.93
		2H	46	Guard	0.165	-0.011	0.315						
			15	Manipulation	0.197	0.002	0.398						
			15	Copulation	0.177	-0.012	0.366						
				Year	0.078	-0.011	0.173	8.35	8.26	20.37	7.85	36.97	18.67
		3H	46	Guard	0.149	-0.032	0.294						
			15	Manipulation	0.193	-0.033	0.372						
			15	Copulation	0.174	-0.011	0.375						
				Year	0.071	-0.029	0.170	9.96	9.06	17.68	7.63	36.70	20.47
2	2	1All	84	Guard	-0.262	-0.411	-0.101						
			12	Copulation	0.267	-0.011	0.488						
				Year	0.017	-0.107	0.120	5.87	35.68	39.78		81.32	
		2All	97	Guard	-0.247	-0.396	-0.073						
			12	Copulation	0.254	-0.000	0.491						
				Year	0.030	-0.071	0.150	4.59	43.10	34.11		81.80	
		3All	97	Guard	-0.211	-0.371	-0.053						
			12	Copulation	0.270	-0.019	0.491						
				Year	0.037	-0.078	0.148	7.15	40.48	32.07		79.71	
		1 Guard	22	Age	-0.360	-0.556	-0.119						
			16	Color	-0.089	-0.459	0.269						
			4	Hormone	0.231	-0.249	0.650						
			11	Polygyny	-0.419	-0.710	-0.039						
			24	Size	-0.233	-0.509	0.016						
			7	Song	-0.354	-0.634	0.038						
				Year	-0.049	-0.186	0.078	4.41	49.56	27.81		81.79	
		2 Guard	26	Age	-0.349	-0.550	-0.158						
			18	Color	-0.053	-0.336	0.255						
			4	Hormone	0.241	-0.251	0.613						
			11	Polygyny	-0.397	0.699	-0.005						
			31	Size	-0.215	-0.437	0.025						
			7	Song	-0.326	-0.574	0.025						
				Year	-0.039	-0.157	0.010	3.48	54.07	24.81		82.35	
		3 Guard	26	Age	-0.312	-0.524	-0.084						
			18	Color	0.058	-0.290	0.366						
			4	Hormone	0.273	-0.208	0.647						
			11	Polygyny	-0.391	-0.662	0.055						
			31	Size	-0.138	-0.359	0.125						
			7	Song	-0.376	-0.637	-0.029						
				Year	-0.026	-0.156	0.124	5.50	53.65	19.76		78.90	
2	4	1E	84	Guard	-0.249	-0.473	0.032						
			12	Copulation	0.271	-0.021	0.560						
				Year	0.011	-0.110	0.116	6.12	32.69	41.34	9.12	7.89	36.46
		1H	84	Guard	-0.243	-0.498	0.015						
			12	Copulation	0.275	-0.051	0.534						
				Year	0.014	-0.096	0.132	5.98	32.08	42.03	9.37	80.09	35.74

Q	M	Data set	k	Paternity protection	Mean (r)	L CI	U CI	I^2_{study}	I^2_{species}	$I^2_{\text{Effect size}}$	I^2_{phylo}	I^2_{total}	H^2
3	2	1	2	Guard	0.157	-0.717	0.828						
			27	Manipulation	0.333	-0.027	0.613						
			9	Copulation	0.042	-0.551	0.583						
				Year	-0.196	-0.498	0.154	17.16	19.66	13.84		50.66	
	4	1E	2	Guard	0.169	-0.704	0.905						
			27	Manipulation	0.337	-0.131	0.677						
			9	Copulation	0.060	-0.546	0.601						
				Year	-0.209	-0.485	0.172	17.11	19.54	14.16	20.50	50.81	26.13
		1H	2	Guard	0.149	-0.740	0.840						
			27	Manipulation	0.350	-0.069	0.699						
			9	Copulation	0.062	-0.564	0.614						
				Year	-0.199	-0.509	0.194	17.39	20.47	13.91	19.98	51.77	26.95

Table S3. Results from the multilevel meta-analyses for each of the questions (Hackett phylogeny), paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care, for Model 3 (phylogenetic null model). Q = question, M = model, k = the number of effect sizes, m = the number of species and n = the number of broods. L. CI and U. CI are the lower and upper confidence intervals respectively.

Q	M	Data set	k	m	n	Mean (r)	L. CI	U. CI	I^2_{study} (%)	I^2_{spec} (%)	I^2_{ES} (%)	I^2_{phylo} (%)	I^2_{total} (%)	H^2 (%)
1	3	1H	76	31	1144	0.175	0.012	0.327	17.11	12.35	10.56	10.69	50.71	24.59
		2H	81	32	1199	0.168	0.005	0.309	19.52	10.19	9.41	9.16	48.27	21.19
		3H	81	32	1199	0.169	0.016	0.306	24.06	10.38	8.53	8.48	51.45	20.34
2	3	1H	96	28	2262	-0.044	-0.373	0.388	3.94	40.57	19.20	21.11	84.82	47.82
3	3	1H	38	15	869	0.219	-0.241	0.588	6.86	13.56	58.19	13.75	92.36	14.66

Table S4. Results from the phylogenetic multilevel meta-analyses (Hackett phylogeny) for each of the questions, paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care, for Model 4 (phylogenetic multi-level meta-regression). Q = question, M = model, *k* = the number of effect sizes, *m* = the number of species and *n* = the number of broods. L. CI and U. CI are the lower and upper confidence intervals respectively.

Q	M	Data-set	*k*	Paternity protection	Mean (*r*)	L. CI	U. CI	I^2_{study}	I^2_{species}	$I^2_{\text{Effect size}}$	I^2_{phylo}	I^2_{total}	H^2
1	4	1	46	Guard	0.201	0.031	0.366						
			15	Manipulation	0.187	-0.037	0.394						
			15	Copulation	0.186	-0.030	0.371						
				Year	0.086	0.001	0.173	17.73	14.95	11.86	9.23	44.55	26.95
		2	51	Guard	0.172	0.014	0.328						
			15	Manipulation	0.202	-0.037	0.372						
			15	Copulation	0.172	-0.035	0.338						
				Year	0.079	-0.013	0.164	18.94	12.39	10.18	7.92	41.51	24.37
		3	51	Guard	0.163	-0.007	0.317						
			15	Manipulation	0.198	-0.027	0.382						
			15	Copulation	0.169	-0.039	0.345						
				Year	0.072	-0.031	0.156	24.41	11.89	10.06	7.99	46.36	21.40
2	4	1	84	Guard	-0.232	-0.474	-0.016						
			12	Copulation	0.259	-0.091	0.509						
				Year	0.029	-0.078	0.141	8.21	44.09	24.56	9.76	76.87	50.43
		2	97	Guard	-0.227	-0.480	0.015						
			12	Copulation	0.254	-0.033	0.528						
				Year	0.030	-0.080	0.139	8.81	43.13	24.10	10.04	76.05	49.63
3	4	1	2	Guard	-0.250	-0.910	0.758						
			27	Manipulation	0.404	-0.138	0.740						
			9	Copulation	-0.075	-0.614	0.541						
				Year	-0.253	-0.524	0.108	7.49	13.24	69.34	16.28	90.06	12.79

Table S5. Results of Egger's regression tests and trim-and-fill (TAF) tests for the multilevel meta-analyses (Hackett phylogeny). Paternity protection in relation to: Question 1 – paternity, Question 2 – male quality, Question 3 – paternal care for Model 3 (phylogenetic null model). L. CI and U. CI are the lower and upper confidence intervals respectively.

Question	Model	Data-set	*t, Egger's*	*Df* (t)	*p* (*t*)	*Missing k: TAF*	Mean (*r*)	L. CI	U. CI
1	3	1H	0.902	74	0.370	0			
2	3	1H	0.344	94	0.732	11	-0.056	-0.120	0.009
3	3	1H	0.568	36	0.574	0			

Conclusion

One of the interesting outcomes of my thesis is the importance of including both male and female roles in models. Many models assume asexual populations without age or other life history structures. This is completely appropriate as selective pressures can act in a comparable manner on individuals independent of sex or age. For example, in chapter 3 sex specific dispersal rates did not evolve because there were no sex specific selective pressures. For chapter 4 we did not include sex specific arrival timing, even though in many species males arrive before females, in this chapter this is appropriate as for both sexes the selection on early arrival is strong (Smith and Moore 2005) and we were interested in the average population arrival time.

However, in many species males and females do not have the same requirements potentially leading to sexual conflict over traits and optimal strategies (e.g. Cox and Calsbeek 2009). Chapter 2 highlights how taking differences between the sexes into account can have important implications for population dynamics. Although it shows that in a polygynous breeding system the evolution of female advantageous alleles is good for population survival, there are severe implications for the populations where these alleles are not advantageous to females.

In the first chapter we approach mate-guarding only from the male perspective — females are only included as passive components of the ASR. This is not because we consider the female perspective as unimportant, indeed females are expected to influence male mate-guarding behavior. For example, in many species there may be sexual conflict over the optimal guarding duration (e.g. Yamamura and Jormalainen 1996; Jormalainen 1998; Westneat and Stewart 2003) however there are also species in which the female has additional benefits from being guarded thus selecting for cooperation (e.g. Rodríguez-Muñoz et al. 2011). In the last chapter of this thesis the female role is considered more extensively in relation to mate-guarding, one of the two types of presumed paternity protection behaviors in birds (the other being frequent copulation). First of all we consider that males of high quality are preferred as mates and that males of high quality may thus potentially expect more cooperation with paternity protection. And second, we highlight a number of ways in which females may influence the different aspects of the relationships associated with paternity.

All the chapters in my thesis have either used a theoretical approach or existing data (i.e. meta-analysis). Using simulation models and other theoretical approaches has many benefits, one can research facets of animal behavior that are difficult to study in the wild.

For example, predation has been studied as a selective force on migratory birds (e.g. Sillett and Holmes 2002), however the impact it may have upon arrival phenology has not. It is likely that this has not been done because it is hard to assess whether a bird has been predated or if it has simply moved on to another breeding area, although we do have such information for species of other taxa (e.g. Williams et al. 1993; Devito et al. 1998). This makes our research novel as it is to our knowledge the first to suggest that predation on birds upon arrival at the breeding ground may affect phenology.

Another benefit of a theoretical approach is being able to examine a large number of parameter combinations. In an empirical experimental approach the number of parameter combinations is often limited by factors such as development time of the species, space for housing and animal ethics. Although being able to examine a large number of parameter combinations is obviously a clear advantage of modelling, a model will always remain a simplification of a natural system.

In conclusion, this thesis highlights the importance of demography for the evolution of breeding strategies. In the first chapter we demonstrate how the ASR can influence the male mate-guarding strategy and shape the evolution of mating systems. The second, third and fourth chapters examine the effects of movement on breeding strategies. The decision and timing of this movement can largely determine an individuals reproductive success and may even have severe implications for a population as a whole. The final chapter explores the use of paternity protection strategies in birds and additionally highlights the complexity of natural systems and the sheer volume of information that complicate these seemingly simple behaviors.

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